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The Herpetofauna of the Guatemalan Plateau, with Special Reference to its Distribution on the Southwestern Highlands

by
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INTRODUCTION

IN a recent study on the geography of the herpetofauna of Alta Verapaz, Guatemala, it was noted (Stuart, 1950:69–70) that there exists in northern Central America in general and in Guatemala in particular three herpetological assemblages. These were named the Caribbean assemblage, the Pacific assemblage, and the Plateau assemblage. The Caribbean is now relatively well known, having been described in the writings of Gaige (1936), Smith (1938), Schmidt (1941), and Stuart (1934, 1935, 1948*b*). There are available, moreover, studies on the local distribution of that assemblage in areas in which it comprises the major part of local herpetofaunas. Of these may be mentioned Ruthven's studies on Veracruz, Mexico (1912, 1913), and my investigations of the Petén, Guatemala (1935), and of Alta Verapaz, Guatemala (1950). Of the Pacific assemblage little is known, although I have a large collection, assembled in 1949, which is now being studied. No general account of the Plateau assemblage has yet appeared, and my purpose in this paper is to present such an account and to describe the local distribution of the Plateau assemblage in a typical highland habitat, the southwestern highlands of southern Guatemala (see Map 1). A list of collecting localities (Appendix I) and an annotated list of species (Appendix II) are included.

To state that we are wholly uninformed as to the nature of the Plateau assemblage would be to belie the facts. Indeed, much of the material brought together by Salvin and Godman and by the French *Mission scientifique au Mexique* originated from these southwestern highlands. More recently the California Academy of Sciences and the Chicago Natural History Museum have supported expeditions into the same area. Accounts of the material secured by these workers have already appeared in scattered sources, notably Günther (1885–1902), Duméril, Bocourt, and Mocquard (1870–1909), Brocchi (1881–83), Slevin (1939, 1942), and Schmidt (1936).

The data upon which this paper is based have been derived from several sources. First, material listed by previous workers, reference to which has been incorporated in the synonymies in the annotated List of Species (Appendix II); very little of this material has been re-examined, and none of it is recorded in the lists of specimens examined, even when such data are available. Second, material contained in various museums of this country which until now has not been reported; an effort has been made to assemble this material in its entirety and to include it in the annotated List of Species with the exception of the amphibians collected by Mr. Joseph Slevin in Guatemala during the years 1924 and 1926. (Mr. Slevin has informed me that he hopes to publish these data in the near future.) Finally, the material which comprises the bulk of the data, my own collection, was assembled largely in 1947 and to a lesser extent in 1944 and 1949.

Material collected by earlier investigators stemmed primarily from the region between Tecpán and Quezaltenango (see Map 2), but especially in and about the former. For that reason I devoted most of my time on the highlands of Guatemala to investigating the mountains north of San Marcos, an area which had previously been unexplored herpetologically. As a result the southwestern highlands may now be said to be fairly well known. The highlands of northern Central America as a whole are as yet poorly known in herpetological literature. This is particularly true of the Sierra de los Cuchumatanes, the Sierra de las Minas, and the Sierra de las Nubes of Guatemala, the higher ridges of Honduras, and the Chiapas highlands of Mexico. In my consideration of the entire Plateau assemblage I have drawn freely from such data as have already been published on these areas, particularly Stuart (1943*b*, 1948*b*), Smith and Taylor (1945, 1948), and Dunn and Emlen (1932).

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Plates I and II and the drawings of the tadpoles on Plate VII were executed by William Brudon, artist of the Museum of Zoology, University of Michigan.

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NATURE OF THE PLATEAU HERPETOFAUNA

Knowledge of the Plateau assemblage of Guatemala and northern Central America is still incomplete, for the genetic relationships of many of the groups are only imperfectly known and in most instances the subspecific phases of their systematics remain to be worked out in detail. Furthermore, the geographic extents of the majority of the forms are as yet only poorly defined, especially wherever the assemblage as a whole encounters the lower elevations that prevail through Honduras and Nicaragua. In its broader aspects, however, the assemblage does lend itself to definition and description, and sufficient data are available to block out its major characteristics.

As I conceive it, the Plateau assemblage is made up of a group of fifteen genera which include representatives of some seventeen supraspecific groups. These may be listed as follows:

GENUS	GROUPS OR SPECIES
Magnadigita	*dunni* and *morio* groups
Pseudoeurycea	*rex*
Bufo	*bocourti*
Plectrohyla	*guatemalensis* and *sagorum* groups (in part)
Rana	*palmipes* group (in part)
Hypopachus	*inguinalis* group
Sceloporus	*formosus* group (in part)
Anolis	*crassulus* group
Abronia	*vasconcelosii, ochoterenai, auritus,* and others
Barisia	*moreleti* group
Thamnophis	*"sumichrasti"* group (in part)
Geophis	*rhodogaster*
Rhadinaea	*godmani* group
Tropidodipsas	*fischeri* group
Bothrops	*godmani*

In addition to this list there are several species or species groups which future investigations may add to the Plateau assemblage. From the data now available, I cannot be certain whether or not they should be included. Along the mesic slopes of the plateaus of northern Central America there occur upland types which are confined to a relatively narrow vertical zone, and these cannot be allocated to the lowland assemblages, yet at present they are not known to be associated with the Plateau assemblage except in fringing areas. Among these may be included *Chiropterotriton, Magnadigita (franklini* group), *Xenosaurus, Pituophis deppei lineaticollis, Adelphicos (veraepacis* group), *Geophis (nasalis* group), and *Bothrops (nigroviridus* group).

This list of forms should make clear my concept of an assemblage. By it I mean an agglomeration of forms which, regardless of phylogenetic relationships or distribution, appear to be autochthonous to a region. An assemblage may be made up of forms derived from several faunal elements, such as Old Northern and South American, as I have demonstrated for the Caribbean assemblage (Stuart, 1950). It may, furthermore, contain forms the distributions of which are considerably more extensive than is the assemblage's general center of origin. In the Plateau assemblage *Bothrops godmani* is representative of such forms. Finally, it may contain systematic units as large as a genus or as small as a subspecies. The genus *Plectrohyla,* the *godmani* group of *Rhadinaea, Rana macroglossa,* and *Thamnophis eques* *fulvus* are illustrative of the several systematic categories represented in the Plateau assemblage. In the last analysis, autochthony is the basic concept of the present definition of an assemblage.

In characterizing the Plateau assemblage several features are notably apparent. First, and most striking, is its depauperate nature. It seems strange indeed that such plastic genera as *Eleutherodactylus, Hyla, Anolis, Sceloporus,* and *Bothrops* are either lacking or at best are represented by but a single form. Second, all members of the assemblage belong either to the Old Northern element (Dunn, 1931) or to what I have recently called the Autochthonous Middle American element (Stuart, 1950:68). As will be shown these two groups have had very similar histories. It is noteworthy that not a single group belongs to the South American element (*nec* Dunn, 1931; *sensu* Stuart, 1950). The Holarctic element of Dunn is not to be expected in the area to which the Plateau assemblage is confined. Finally, the assemblage is made up almost entirely of groups, of which the centers of distribution are, for the most part, restricted to northern Central America and southern Mexico and which appear to be autochthonous to that same general area. In brief, the Plateau assemblage may be said to be an impoverished agglomeration of groups with an Old Northern or Old Northern-like history, largely endemic to the highlands of northern Central America and southern Mexico, and which have, for the most part, originated *in situ.*

It is not suggested that this assemblage occurs alone wherever it is found. Indeed, it is often mixed with elements derived from both the Pacific and Caribbean assemblages, especially at lower elevations. Conversely, not all the genera or groups are represented, even within the confines of a single life area in which the Plateau assemblage predominates in the herpetofauna. At higher elevations in Alta Verapaz, Guatemala, for instance, the assemblage, though forming a conspicuous part of the herpetofauna, is present in only a dilute form, with such items as *Bufo bocourti, Pseudoeurycea,* and *Geophis* lacking. Finally, as previously suggested, not all the groups listed are confined to the Plateau assemblage. Thus, in northern Central America, the *formosus* group of *Sceloporus,* the *palmipes* group of *Rana,* and the *"sumichrasti"* group of *Thamnophis* are represented as well in either the Pacific or the Caribbean assemblages or both.

As a faunal unit the Plateau assemblage has a relatively small geographic range. Only *Bothrops godmani* and *Magnadigita* (*dunni* group) extend southward and beyond the limits of the highlands of northern Central America, though relatives of some groups or species, such as *Pseudoeurycea,* occur in southern Mexico north of the Isthmus of Tehuantepec. As a clearly defined unit, however, the assemblage is confined to the southwestern, northwestern, and central highlands of Guatemala and to parts of the Sierra Madre and Mesa Central of Chiapas, Mexico. Beyond these limits it persists in only very dilute form.

Within these relatively narrow confines the various genera which have contributed members to the assemblage are known to have undergone no little local differentiation, and even more differentiation will probably be encountered when some of the lesser known highland areas have been more thoroughly explored. Table I, which is a comparison of some of the assemblage's representatives in three highland life areas in Guatemala, brings out the extent of such differentiation.

Within the confines of the highland areas to which the assemblage is restricted, it may be said to range roughly between 1500 and 3600 m. In the southwestern highland area the lower limits are reached by three forms, *Sceloporus malachiticus, Anolis crassulus,* and *Rhadinaea godmani,* while *Pseudoeurycea rex* on Volcán Tajumulco attains a maximum vertical limit of about 4000 m. This volcano, except for one or two others, is the only locale in Guatemala exceeding 3600 m.

The herpetofaunas of the northern Central American plateaus in general and of the Guatemalan section in particular are composed essentially of the Plateau assemblage. On the basis of present knowledge the herpetofauna of the southwestern highlands possesses only a single species, *Rana pipiens,* derived from another assemblage. It is true that in fringing areas several species from other assemblages appear on the southwestern highlands. From the Pacific coast *Ameiva undulata parva* and from the little known interior basins *Sceloporus variabilis olloporus* enter the outlying districts of the southwestern highlands. But these and several others have been unable to establish themselves as components of the herpetofauna that occupies the southwestern highlands proper. Thus, the southwestern highland herpetofauna is almost synonymous with the Plateau assemblage.

This herpetofauna may be arranged into three categories: species and/or subspecies belonging to genera and supraspecific groups which have apparently evolved on the highlands of northern Central America and which remain today strictly highlanders, such as *Plectrohyla, Rhadinaea (godmani* group) ; forms which have been derived fairly recently from exotic ancestors and which have been sufficiently plastic to adjust to highland conditions through differentiation, such as, *Thamnophis eques fulvus* and *Sceloporus malachiticus* subsp.; and forms which through an apparently wide range of tolerance have become firmly established as members of the herpetofauna, such as *Rana pipiens.* This matter will be considered in some detail later in this paper.

PLATEAU HERPETOFAUNA ON THE SOUTHWESTERN HIGHLANDS

Before proceeding with a discussion of the Plateau assemblage as a whole it is necessary to examine its local distribution within a single life area in which it comprises the dominant element of the herpetofauna. On the southwestern highlands of Guatemala the assemblage appears to reach

TABLE I

Local Differentiation of Representatives of the Plateau Assemblage in Three Life Areas of the Guatemalan Highlands

Genus	Southwestern Highlands	Cuchumatán Mountains	Alta Verapaz
Magnadigita (dunni group)	*rostrata*	*rostrata* and *cuchumatana*	*helmrichi*
Plectrohyla (*sagorum* group)	*cotzicensis*	*ixil*	*quecchi*
Hypopachus	*barberi*	*simus*	*inguinalis*
Sceloporus	*m. smaragdinus*	*m. smaragdinus*	*m. taenicocnemis*
Anolis	*c. crassulus*	*c. crassulus*	*c. haguei*
Abronia	*vasconcelosii*	*ochoterenai* expected	*fimbriata* and *aurita*
Barisia	*m. fulva*	*m. temporalis*	*m. moreleti*
Rhadinaea	*godmani*	*stadelmani*	*hempsteadae*
Tropidodipsas	*fischeri*	*fischeri*	*kidderi*

its maximum development, and, from what little data are available for comparisons with other life areas, in this region it occurs in its purest form with little or no mixing with extraneous assemblages. Of all the highland life areas in Guatemala the southwestern is the most distinct, both with reference to faunal and geographic limits, and it possesses many of the major environments characteristic of the uplands of northern Central America. I have previously applied the name Chimaltenangan life area (Stuart, 1942*c* and 1943*a*) to these southwestern highlands.

The Chimaltenangan life area includes all that territory lying above the 1800–2000 m. contour extending from Guatemala City northwestward to the Cuilco-Negro entrenchment and bounded laterally by the escarpment of the Pacific slopes and the broad western limits of the Chuacús-Minas-Mico mountain block (Map 1). Locally, this region is known as "Los Altos," though the western one-third is often considered as a separate entity, the Sierra Madre.

Natural Landscape

Many travelers and scientists have given vivid descriptions of the landscape of the southwestern highlands. Among the best are those of Stephens (1854), Maudslay and Maudslay (1899), and McBryde (1947). For a technical account of the geology, climate, and vegetation, however, Sapper (1937), McBryde (1942 and 1947), and Standley and Steyermark (1945) are all better sources.

In the Mexican-Guatemalan section of "nuclear Central America," the southwestern highlands are but one of nine clearly defined mountain blocks. This block, which is some 200 kilometers in length and generally less than 50 kilometers in width, extends southeastward from the Mexican border to and possibly including the Sierra de las Nubes (a subblock) east of Guatemala City. To the northwest it abuts the Sierra Madre de Chiapas; to the east it is delimited by the Chuacús-Minas-Mico range; to the north the great fault through which flow the Río Cuilco and Río Negro separates it from the blocks of the Sierra de los Cuchumatanes and the Zona Reina; and to the south it drops off sharply in an escarpment to the Pacific coastal plain. On the face of this scarp lies a long line of volcanoes, which everywhere south of the continental divide dominate the landscape.

This mountain block dips from northwest to southeast, attaining its maximum elevation (3700 m.) in the Sierra Madre on Cerro Cotzic; its outliers east of Guatemala City do not greatly exceed 2500 m. in elevation. In the Sierra Madre it consists of a high rolling plateau with some 300 square kilometers of surface above 3,000 m. (Pl. II; Pl. III, Fig. 1). From there to the region of Totonicapán the crest decreases somewhat in elevation, but remains a broad rolling upland. East of Totonicapán this crest narrows rapidly and terminates sharply above Tecpán (Pl. I). In this eastern section the high surface is punctuated with a series of peaks of which Cerro Quiché, with an elevation of slightly more than 3400 m. is by far the highest. East of Tecpán the backbone of the block is visible only as scattered remnants.

Although the protaxis of this block, like that of all of nuclear Central America, was developed prior to the Carboniferous, it was the great Pliocene orogeny that elevated it to its present height. At that time the whole region was overflowed with andesites and the whole was later covered with a deep layer of volcanic ash which was thrown out by Pleistocene volcanoes.

Subsequent erosion has produced the rugged, barranca-cut surface which, especially in the east, characterizes its extant topography. So active has been the work of running water that the western third of the block has been almost completely divorced from the remainder of the mountain mass by the headwater cutting of the Río Cuilco, and it is joined today to the more extensive highlands to the east by only a narrow bridge in the region of Serchil. This western section is locally recognized as a separate entity, the Sierra Madre.

Erosion, either owing to greater rainfall or to the greater depth of the ash mantle, has been most active east of Totonicapán. From there eastward to Guatemala City and especially south of the continental divide, the upland surface is slashed by great, steep-sided barrancas of which some must exceed 500 m. in depth. The terrain west and north of Totonicapán, although cut by numerous river valleys, is less rugged in character, and the highland surface presents more subdued features. This is especially true of the highlands in the region of Sija and of the plateau surface of the Sierra Madre.

In his excellent discussion of the climate of southwestern Guatemala, McBryde (1942), though lacking data for the greater part of the region here considered, presented a most logical interpretation of conditions. Except for possibly the very highest peaks, the climate of the southwestern highlands may be classified as *Cw*, according to the Köppen system. This simple allocation to type does not, however, bring out the diversity and complexity of the microclimates occurring within the region.

It is doubtful that any part of the area experiences a mean annual temperature as high as 18°C. and certainly the warmest month, May, does not exceed 20°C. Scattered records indicate that the extreme maximum temperature any place in the area is probably less than 30°C. At the lower limits (1800 m.) the southwestern highlands probably have means in the neighborhood of 20°C. and 15°C., for the hottest and coldest months, respectively. At the very highest elevations in the Sierra Madre these same means are undoubtedly reduced to about 10°C. and 5°C., the former figure representing the *E* boundary of Köppen. At Ixchiguán, in April and in

June of 1947, I recorded diurnal minimums of 4° to 5°C. and an average diurnal maximum of 15°C.

Rainfall records, like those for temperature, are almost entirely lacking for most of the region. None of the region, however, suffers from a rainfall deficiency. Above about 1500 m. on the Pacific versant rainfall decreases sharply from a maximum of over 5000 mm. annually to as little as 670 mm. in the sheltered basin of Quezaltenango (*ca.* 2500 m.). Just what conditions prevail at higher elevations on the ridges where the volcanoes offer less protection is unknown. The south side of the continental divide at elevations above 2000 m. is subjected to almost daily fog blankets and, though possibly receiving no great amount of rainfall, must be extremely humid. North of the divide somewhat drier conditions evidently prevail, for at Chichicastenango in 1945, the only year when records were kept, the rainfall amounted to only 1300 mm. The dryness of the oak-pine forest, which is the dominant cover to about 2500 m. over most of the area, is probably as much owing to the porous nature of the volcanic ash as it is to the low rainfall. The humid forests which are above 2700 m. are favored not only by the heavy fogs but by a greatly reduced precipitation-evaporation index as well. At least 85 per cent of the rainfall comes during the period May through October.

McBryde's (1947) fine plan of the natural vegetation of southwestern Guatemala, though occasionally incorrect in local detail, provides an excellent outline of the flora of the region. Insofar as the highland section is concerned, his scheme of the major floral types may be summed up as follows:

1800–2500 m., oak-pine zone
2500–2700 m., pine-bunchgrass zone
2700–3100 m., pine-cypress-bunchgrass zone
Above 3100 m., alpine meadows

To these four major types may be added two very local cover types, the short-grass plains of the Quezaltenango Basin and the localized chaparral of the Zunil region. Timberline, according to McBryde, lies at approximately 4000 m. and is attained only on the volcanoes Tacaná and Tajumulco.

The presence of a large human population on the highlands, concentrated in the oak-pine zone, has resulted in extensive clearing of the virgin forests of that area. There remain, however, many fine stands of oak, pine, and mixed forest throughout the entire region. Some forests may be virgin, but others are definitely second-growth stands, which have developed the climax type over abandoned clearings (McBryde, 1947: 19). The forests ordinarily occur in groves interspersed through the cultivated fields and pastures (Pl. V, Fig. 2), but in some areas they are restricted to the hilltops and to the steeper slopes. The most extensive unbroken forest on the highlands, to my knowledge, is that which extends northward from Momostenango toward the valley of the Río Negro.

There is not complete uniformity in the distribution of the several forest types which characterize the oak-pine zone. In some areas, such as the vicinity of Momostenango, there are extensive stands of almost pure pine, whereas on the rocky slopes of the headwaters of the Río Cuilco near Tejutla oak is the dominant cover. The pine forests are generally of the open variety with little underbrush. There is usually a deep layer of needles, though occasionally these forests assume a parklike character, and grassy slopes replace the needle-covered floor (Pl. VI, Fig. 1). Such pine forests may be classified as *Emc.Gc* by the Küchler system (1949). In contrast, the oak forests support a somewhat heavier undergrowth, and the ground is generally covered with a mantle of dead leaves, which often accumulate in great quantities in the smaller ravines (Pl. VI, Fig. 2). This type of forest may be indicated by the formula *Dlsi.Hc/p*. Since they serve as the main source of fuel, few logs are left to rot in forests that lie in proximity to large Indian concentrations, as in the Momostenango or Tejutla regions, and woodcutters generally leave the unusable twigs and smaller branches in neat piles. In the river bottoms of the oak-pine zone and along ravines a denser and more mesic type of forest prevails. Here a broadleaf forest, which in the valleys on the flanks of the Sierra Madre is composed of willow, cherry, and alder, often forms a rank growth which may develop into almost impenetrable thickets *(Dlsc)*.

The pine-bunchgrass zone of McBryde seems to represent a transitional area. In many places it is not visible as a distinct entity. The limits as defined by McBryde are at best only approximate. Where I have seen this zone, it appears to be an area in which the oak gradually drops out and the bunchgrass (*pajón*) becomes a dominant feature of the cover.

I am not certain that the subdivision of the higher elevations is completely warranted. As a definite cover type, the pine-cypress-bunchgrass is certainly distinct, but McBryde's "alpine meadow" is not too clearly recognizable. In the Sierra Madre, which he maps as the largest single area of alpine meadow, the forests, bunchgrass plains, and the short-grass plains seem to be coincidental in their vertical limits. As a rule, the region above 2700 to 3000 m. supports a cover of all three types. The forests at lower elevations tend to be pine (Pl. IV, Fig. 2) or mixed pine-cypress, whereas on the higher ridges almost pure stands of pine predominate. These forests are extremely wet and dense, and consequently support little undergrowth, though the forest floor is generally strewn with the rotting moss-covered trunks and branches of fallen trees (Pl. V, Fig. 1). According to the Küchler system they are *Emc.Hp/c*. In places such as the crest of the Sierra Madre (Pl. IV, Fig. 1), the forest thins out and takes on a parklike aspect *(Emi.Gm/lc)*. Interspersed with the forests are the bunchgrass plains *(Gmc)*, which to the west of Totonicapán far exceed the forests in extent (Pl. III, Fig. 1). Short-grass plains *(Glc/p)* are most frequent on the rock fields of the Sierra Madre and generally take over clearings from which the bunchgrass has been dug, either for its roots or to make room for the cultivation of potatoes (Pl. III, Fig. 2). In such areas the cover may consist of herbs and low bushes in addition to the short grasses *(Ds.Gl)*. I am inclined to view the pine-cypress-bunchgrass zone and the alpine meadows as a single vegetational zone, which is characteristic of the highlands above 2700 to 3000 m. elevation.

The short-grass plains of the Quezaltenango area are of but slight extent. They are restricted to the broad floodplain of the Río Samalá and its tributaries, and the pine forest on the sides of the valley has a sharply defined boundary along the base of the slopes. These plains are either intensively cultivated in wheat or form lush pastures.

The chaparral of the Zunil region is too localized to warrant discussion. It is characteristic of rain-shadow areas along the Pacific versant and supports a dense thicket-like cover of scrubby bushes and oak. It predominates also in the Panajachel region at 1500 m. In general aspect the oak-pine zone may be classified as *EDmp.Gm* and the pine cypress as either *Emp.Gm* (María Tucum) or *Gmc.Emp* (Sierra Madre).

The most significant departures from the vertical limits suggested by McBryde are on the eastern, northern, and western flanks of the Sierra Madre, where sheltered valleys cause the isopleths to lie at somewhat higher elevations than they do in more exposed situations. As a result the generalized scheme outlined above breaks down when examined in detail. Nevertheless, the oak-pine and pine-cypress-bunchgrass zones are readily recognizable as entities and the variation in their vertical limits from place to place is taken up at the expense of the more or less transitional pine-bunchgrass belt.

Herpetofauna of the Southwestern Highlands

Analyses of the herpetofaunas of various highland areas in Guatemala reveal that the southwestern highlands support an assemblage of reptiles and amphibians which, though small, is distinct. Although twenty-four forms are recorded from the area, only nineteen can be considered true Chimaltenangan species (Appendix II). No less than nine of these proved to be endemic to the area: *Magnadigita morio, Plectrohyla cotzicensis, Plectrohyla guatemalensis, Hypopachus barberi, Abronia vasconcelosii, Barisia moreleti fulva, Rhadinaea godmani, Geophis rhodogaster.*

Some of these endemic species spill over slightly into adjacent life areas, but this extension of range beyond the limits of the Chimaltenangan life area, as previously defined, is negligible.

Overlying this endemic element is a group of forms which is more widely distributed over the highlands of Guatemala or northern Central America, especially the Cuchumatán area (Stuart 1942*c* and 1943*a*) to the north. In this group may be included: *Magnadigita rostrata, Pseudoeurycea rex, Bufo bocourti, Anolis crassulus crassulus, Sceloporus malachiticus smaragdinus, Thamnophis eques fulvus, Tropidodipsas fischeri.*

Only three species which are typically a part of the southwestern highland fauna have ranges of any great extent: *Rana macroglossa, Rana pipiens* (s. l.), *Bothrops godmani.*

A single form, *Barisia moreleti rafaeli,* occurring in the Sierra Madre in the extreme western section of the area represents an integrading population more than it does a typical form. It is obviously an approach to the typical *rafaeli,* which is apparently endemic to the Sierra Madre of Chiapas, Mexico.

Five other forms are on the fringes of the southwestern highlands, where contact is made with adjacent life areas. These are not considered typical members of the Chimaltenangan fauna: *Anolis laeviventris, Sceloporus variabilis olloporus, Ameiva undulata parva, Pituophis deppei lineaticollis,* and *Rhadinaea lachrymans.*

All genera or species groups characteristically considered a part of the Plateau assemblage are represented in the fauna of the Chimaltenangan life area and, aside from the several fringing exotics and *Rana pipiens,* no other elements are included in its fauna.

Southwestern Highland Herpetofauna as an Entity

Annectent to other highland areas the herpetofaunas of which are predominantly drawn from the Plateau assemblage, it is surprising that the Chimaltenangan fauna should be so readily differentiated as a unit. As yet it cannot be demonstrated that the fauna of the southwestern highlands is uniformly distributed over the Chimaltenangan faunal area. Neither *Magnadigita morio* nor *Hypopachus barberi* have been secured in the Sierra Madre section of the west, and *Barisia moreleti* is represented in the west by a population which closely approaches *rafaeli* rather than the typically Plateau form *fulva.* It is entirely possible that differences in collecting techniques or seasonal variations in collecting time account for several of these observed faunal differences. Nevertheless, the fauna's intraregional homogeneity is far greater than any similarity the fauna may exhibit to those of annectent regions.

Though still only incompletely known, there is sufficient evidence to indicate that the southwestern highland fauna resembles most closely that of the Sierra de los Cuchumatanes to the north, especially insofar as the fauna of their higher elevations is concerned. With the Cuchumatán area (Stuart, 1942*c*, 1943*a*, and 1943*b*) it shares the following species: *Magnadigita rostrata, Pseudoeurycea rex, Bufo bocourti, Anolis crassulus crassulus, Sceloporus malachiticus smaragdinus* (in part), *Thamnophis eques fulvus, Tropidodipsas fischeri.*

Several genera present in the two areas, however, are represented by different species or subspecies:

GENUS	CHIMALTENANGAN	CUCHUMATAN
Magnadigita	*morio*	undescribed species
Plectrohyla	*cotzicensis*	*ixil*
Hypopachus	*barberi*	*simus*
Barisia	*m. fulva*	*m. temporalis*
Rhadinaea	*godmani*	*stadelmani*

In addition to these differences, the Sierra de los Cuchumatanes supports, especially on its very wet eastern and northeastern slopes, a number of species unknown to the southwestern highlands. Among these may be mentioned *Magnadigita lincolni,* several species of *Hyla,* one of *Eleutherodactylus,* and several genera, notably *Dryadophis* and *Adelphicos,* of snakes which, though known from higher elevations on the Pacific versant, do not enter the southwestern highlands. In spite of certain similarities in the faunas of the two areas, the local endemism and the more diversified fauna of the Cuchumatán area serve to separate the two regions faunally.

Between the Cuchumatanes and the southwestern highlands are the arid to semiarid headwater valleys of the Rios Cuilco, Saleguá, and Negro. These valleys appear to be a major barrier to free intercourse between the highland faunas to the north and south of them and certainly support a herpetofauna very different from that of the highland areas which they separate. Typical species are: *Bufo marinus, Anolis sericeus, Sceloporus variabilis olloporus* (or *v. variabilis*), *Sceloporus melanorhinus stuarti, Basiliscus vittatus, Ctenosaura similis, Cnemidophorus deppii deppii, Conophis pulcher pulcher, Oxybelis aeneus auratus.*

Wherever headwater streams of the Cuilco and Negro river systems cut back into the highlands of the Chimaltenangan area, the more tolerant forms of this xeric fauna invade the fringes of the southwestern highlands to considerable elevations. At Momostenango, for example, *Sceloporus variabilis olloporus* was secured at 2200 m.

Further study will probably reveal that this xeric fauna is either the same as, or closely allied to, that of the desert valleys of central Guatemala, which were previously named the Zacapan life area (Stuart, 1942*c* and 1943*a*; Schmidt and Stuart, 1941). Though definite data are lacking at this time, I have reason to believe that these valleys form the connecting link between the arid Motagua Valley and interior desert basins of Guatemala and the equally xeric Chiapas Valley through which the subhumid Tehuantepec region may be reached.

The highlands adjoining the Chimaltenangan faunal area to the east make up the Chuacús-Minas-Mico mountain range. From this area, the Sierran of Stuart (1942*c* and 1943*a*), have come only a handful of specimens. It is entirely possible that many species of the Plateau assemblage occur in the region, but, like the Cuchumatán area, these mountains support a number of species unknown on the southwestern highlands. Worthy of mention are *Hyla spinipollex, Eleutherodactylus* sp., *Centrolenella fleischmanni,* and *Lygosoma cherriei cherriei.* More thorough investigations of the area, will, it is believed, reveal that its fauna has more in common with that of Alta Verapaz than with that of the southwestern highlands.

Toward the southeast in the vicinity of Guatemala City, the highlands become considerably lower, and only the Las Nubes block attains elevations comparable to those of the west. Though I had previously included the southeastern highlands, in part, with the southwestern highlands (Stuart, 1942*c* and 1943*a*), I am now convinced that the two have little in common. Over most of this southeastern area lowland types predominate, as may be seen by the occurrence of such forms as: *Oedipina uniformis* (or an undescribed relative), *Bufo marinus, Engystomops pustulosus, Leptodactlyus melanonotus, Sceloporus variablis olloporus, Basiliscus vittatus, Ameiva undulata parva, Leptodeira annulata polysticta, Leptoderia rhombifera.*

Members of the Plateau assemblage occur at higher elevations in the southeastern area, for on the Las Nubes block may be found: *Rana macroglossa, Plectrohyla guatemalensis, Anolis crassulus crassulus, Sceloporus malachiticus malachiticus, Thamnophis eques fulvus, Bothrops godmani.*

Despite the occurrence of many forms of the Plateau assemblage in the southeastern region, the fauna of the area as a whole is much richer than that of the southwest, and the two are obviously different. It may be noted that this somewhat lower region in eastern Guatemala perhaps affords a pathway, across which the more tolerant species of the Caribbean and Pacific lowland assemblages have free movement.

On the south the Chimaltenangan area contacts the Pacific versant, which includes the scarp face and the associated volcanoes and has previously been designated the Fuegan life area (Stuart, 1942*c* and 1943*a*). My recent investigations indicate that a complex faunal arrangement obtains in the Fuegan area. Though most of the area west of Escuintla is excessively humid, there occur on the slopes several protected valleys which are semiarid or at least very much drier than the unprotected slopes. Because of this variation the herpetofauna of the Pacific versant as a whole lacks uniformity and generalizations are difficult. Regardless of the faunal affinities of the region, which are beyond the scope of this paper, the Pacific versant fauna has little in common with that of the southwestern highlands. A list of the commoner and more characteristic forms of the humid slopes would include: *Magnadigita franklini, Bufo canaliferus, Eleutherodactylus matudai, Plectrohyla matudai, Centrolenella fleischmanni, Anolis cupreus, Leiolopisma assatum assatum, Drymobius chloroticus, Drymobius melanolomus stuarti, Ninia sebae sebae, Adelphicos quadrivirgatus sargii, Micrurus nigrocinctus zunilensis.*

A few species highly characteristic of the humid slopes enter the Chimaltenangan area along its fringes: *Ameiva undulata parva, Pituophis deppei lineaticollis, Rhadinaea lachrymans,* and *Geophis nasalis.*

Conversely, some of the species typical of the southwestern highlands spill over on the humid slopes at higher elevations. Thus, associated with such typical slope forms as *Magnadigita franklini, Plectrohyla matudai,* and *Rhadinaea lachrymans,* in the cloud forest of the Pacific versant at Lorena, are such Plateau assemblage forms as *Bufo bocourti, Anolis crassulus crassulus, Barisia moreleti fulva,* and *Tropidodipsas fischeri.*

In the subhumid valleys of the slopes an even stronger representation of Chimaltenangan forms is found. From the Antigua Basin, in addition to the typically slope species, the following Plateau forms are known: *Rana macroglossa, Anolis crassulus crassulus, Sceloporus malachiticus smaragdinus, Thamnophis eques fulvus, Rhadinaea godmani.*

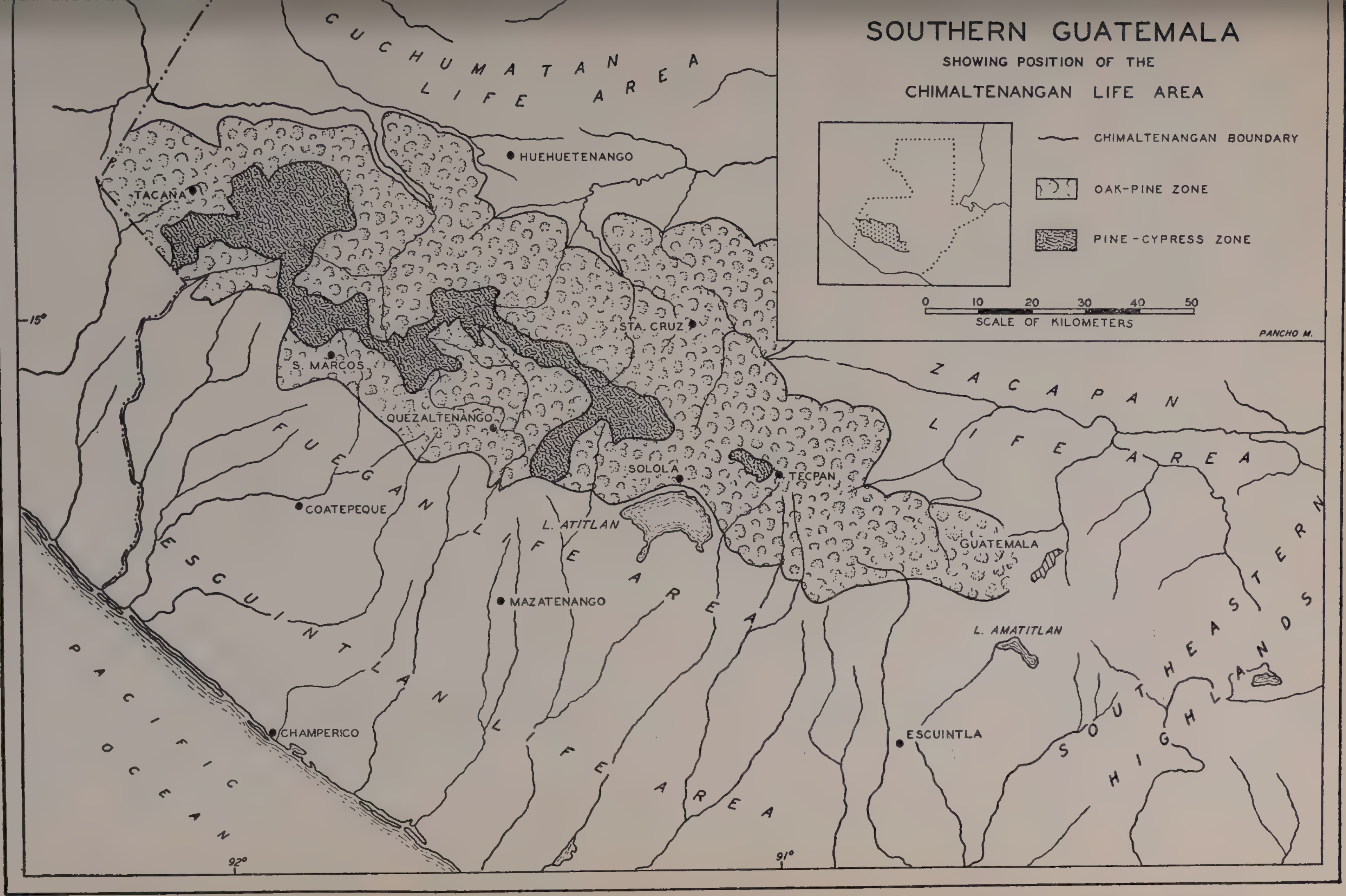
Despite the fact that a number of the species of the Chimaltenangan and of the Fuegan are shared by both areas along their common boundary, the fauna of the latter is essentially derived from the Pacific assemblage and viewed *in toto* is very different from that of the former. Only along the line of contact between the two regions is there any great amount of faunal overlap.

In summation it may be said that a small but recognizable fauna inhabits the southwestern highlands of Guatemala. There is a slight tendency for this fauna to descend to relatively low elevations in the more arid environments of adjacent areas and for a few of the more tolerant species of some of the surrounding regions to invade the fringes of the southwestern highlands when the environments are similar. For the most part, however, the southwestern highland fauna is an entity which serves to characterize the Chimaltenangan faunal area.

Ecologic Distribution of the Southwestern Highland Herpetofauna

With the Chimaltenangan fauna serving as a specific example of the local distribution of the Plateau assemblage, it may be possible to make certain broad generalizations regarding the Plateau assemblage as a whole and the role of the northern Central American highlands in determining the herpetofauna agglomerations to the north and south. It is axiomatic that only through a detailed knowledge of the local distribution of a fauna can its nature and origin be explained.

In a mountain area the basic geographic lineaments are arranged vertically rather than horizontally. Except for forms considered not typical of the fauna of the southwestern highlands and with allowance for slight faunal differences between the eastern and western assemblages, the following species have been secured from elevations ranging from 2000 to 2600 m. (species restricted to this range on the southwestern highlands are marked with an asterisk): **Magnadigita morio, Bufo bocourti,* **Plectro-*



Map 1. Southern Guatemala, giving the limits of the southwestern highlands and the life belts included in that faunal area.

hyla guatemalensis, **Rana macroglossa,* **Rana pipiens,* **Hypopachus barberi,* **Anolis crassulus crassulus, Sceloporus malachiticus smaragdinus, Barisia moreleti* subsp., *Thamnophis eques fulvus,* **Tropidodipsas fischeri,* **Rhadinaea godmani,* **Geophis rhodogaster,* **Bothrops godmani.* Of the fourteen forms included, five are endemic to the Chimaltenangan region, and are restricted to these lower elevations.

The fauna which inhabits higher elevations, that is, above 3000 m., on the southwestern highlands is somewhat smaller than that of lower elevations. Ten of the species characteristic of lower elevations are lost in the higher and but four others are added: **Pseudoeurycea rex,* **Magnadigita rostrata, Bufo bocourti,* **Plectrohyla cotzicensis, Sceloporus malachiticus smaragdinus, Barisia moreleti* subsp., **Abronia vasconcelosii, Thamnophis eques fulvus.*

In contrast to the fauna of lower elevations, that above 3000 m. contains only two Chimaltenangan endemics, *Plectrohyla cotzicensis* and the poorly known *Abronia vasconcelosii,* which are restricted to it.

Not only are these two agglomerations characteristic of the two vertical zones on the southwestern highlands, but there is also some difference in the density index (number of specimens observed divided by man-hours of observation) in certain species occurring in both zones. Table II records this situation as observed in *Sceloporus malachiticus smaragdinus,* representing conditions observed in comparable habitats in the two zones. Locally, the density index of the species is occasionally much higher than that indicated. Along a small stream at Ixchiguán *Sceloporus* was so abundant that no accurate count could be made, but the density index must have exceeded 500. A comparable condition was also observed along a road through a pine-cypress forest in the vicinity of Serchil. Though fewer in numbers, *Barisia moreleti rafaeli* was more abundant in the Sierra Madre in the upper zone than it was in the lower. An analysis of the factors responsible for this increased population density in the apparently least favorable of the habitats on the southwestern highlands is beyond the scope of this paper.

TABLE II

DENSITY INDEX OF *Sceloporus m. smaragdinus* IN COMPARABLE HABITATS IN THE OAK-PINE AND PINE-CYPRESS ZONES

Habitat	Lower Zone (Tejutla)	Upper Zone (Ixchiguán)
Rocky stream banks	16	59
Rock walls	20	53

The exact vertical limits of these two agglomerations are difficult to establish. It can only be shown, where investigations have been carried on, that each is associated with a definite type of environment; from this it seems reasonable to conclude that the limits of the two assemblages coincide with the limits of the environments in which they have been observed. The fauna of the lower elevations in both the east and the west occurs in the oak-pine vegetational zone and that of the higher elevations in the pine-cypress-bunchgrass vegetational zone. Without more detailed data, therefore, it may be suggested that the agglomeration of lower elevations ranges from the lower limits of the Chimaltenangan area to about 2700 m., above which occurs that of higher elevations. Further investigations will probably reveal that this boundary is at best only a rough approximation and that the two assemblages merge gradually. This floral-faunal relationship is merely a convenient method of defining limits and in no sense implies that vegetation is the limiting factor to the distribution of the herpetofauna.

The local distribution of the fauna within the limits of the two major zones is not particularly complex. In general, the fauna, especially the reptilian, has little or no ecologic relationship to the major features of the environment, such as geomorphological features or vegetation. Rather, the various species are arranged in a geographic pattern that is determined by some minor environmental factor related to their habits.

Within the oak-pine zone there are two major ecologic types, the aquatics and near-aquatics and the terrestrials. The aquatic and aquatic margin habitat types support a fauna which is composed basically of amphibians, with reptiles only represented in situations in which environmental conditions other than water fortuitously prevail. The following five species are dependent upon the aquatic environment during all or a part of their life cycles: *Bufo bocourti, Plectrohyla guatemalensis, Rana macroglossa, Rana pipiens, Hypopachus barberi.*

Of these only *Plectrohyla guatemalensis* and the ranas are entirely aquatic; the other two are restricted to water only during their larval stages.

The lotic habitat is far better developed than is the lenitic, and, as a result, its members are more widely and more uniformly distributed throughout the area. The lenitic environment is at best only poorly developed and sparsely distributed in this mountainous region, so that it is important to emphasize that its restricted fauna includes only *Bufo bocourti* and *Hypopachus barberi,* the two species which are dependent upon water only during the larval period of their life cycles. Though most often associated with the lenitic environment, *Rana pipiens* can and does exist in pools in streams.

In contrast to the lenitic environment, the lotic environment is widely distributed over the southwestern highlands and runs the gamut from the tiny rivulets (*riachuelos*) of the rugged mountain slopes to the large rivers formed at lower elevations. In such habitats *Plectrohyla guatemalensis* and *Rana macroglossa* exist under almost unbelievably severe conditions associated with steep gradient and flash floods.

Notorious as a feeder on salientians, both in their adult and larval forms, *Thamnophis eques fulvus* is commonly associated with the aquatic margin habitat. Where proper conditions prevail fortuitously in the same habitat, other reptilian species may occur. *Sceloporus malachiticus smaragdinus,* a saxicolous species, attains tremendous population densities on rocky flood plains and in boulder-strewn barrancas, and the secretive *Geophis rhodogaster* may be found beneath logs on forested flood plains.

Inasmuch as it is doubtful that open grasslands ever existed as a climax in the oak-pine zone on the southwestern highlands prior to the arrival of man, the terrestrial assemblage of the zone was probably strictly a forest fauna. Yet despite this probability, the distribution of the several species occurring in the region shows surprisingly little geographic relationship to cover. The fauna seems to sort out, rather, into two groups, cryptophiles (secretives) and phanerophiles (nonsecretives), according to the way of life of the various species:

CRYTOPHILES
Magnadigita morio
Barisia moreleti subsp.
Tropidodipsas fischeri
Rhadinaea godmani
Geophis rhodogaster

PHANEROPHILES
Anolis crassulus crassulus
Sceloporus malachiticus smaragdinus
Thamnophis eques fulvus
Bothrops godmani (nocturnal)

Almost any type of shelter appears to provide the cryptophiles with a suitable habitat. They were taken from beneath piles of brush, from leaf accumulations in oak forests, from beneath rotting logs, and from rock piles. Such shelters, moreover, were associated with varied geomorphologic forms and cover types. *Geophis rhodogaster,* for example, was secured from beneath debris in such diverse situations as moist, forested river flood plains, cultivated hillsides, and dry grassy slopes of pine parklands. Only *Magnadigita morio* appears to have a close ecologic relationship to a specific type of cover. Schmidt (1936: 154) reported that Slevin secured this species almost exclusively from beneath bark and rotted stumps of oak at Chichavac, and I observed it under similar conditions on the north slopes of Volcán Acatenango.

Similarly, the phanerophiles were extremely tolerant of varied ecological conditions. *Sceloporus malachiticus smaragdinus,* which is primarily a saxicolous type, was abundant in the rock walls surrounding cultivated fields, among the boulders of rocky flood plains, and especially on the rugged lava fields of the dry north slopes of Volcán Tolimán. *Anolis crassulus crassulus* was most frequent on logs and the lower branches of low bushes along trails through oak thickets, in dense second growth, among bunchgrass clumps on unforested slopes, and in brush-bordered cultivated fields. *Thamnophis eques fulvus,* though most common in the vicinity of water, was encountered under practically any environmental condition. I even secured a specimen of it from beneath a pile of oak branches on a grassy slope, where it was associated with *Rhadinaea godmani* and *Barisia moreleti rafaeli.*

With the population density of the various species of the oak-pine fauna more dependent upon the minor than upon the major features of the environment, it is natural that there should be a tremendous variability in the density index of a species from locality to locality. In regions in which rotting logs are common, the phanerophiles are abundant. Slevin, between July 14 and August 16, 1926, secured in the cutover forests in the vicinity of Chichavac a much larger collection (Table III) than I did in similar situations in the Sierra Madre during some twenty days collecting at various seasons. According to Slevin's descriptions (1939 and 1942) the Chichavac area abounded in forest debris. On the flanks of the Sierra Madre rotting logs, loose bark on the forest floor, and other types of debris are extremely scarce. Even allowing for a possible collecting period of ten days longer for Slevin than for myself, his collecting in the Chichavac area was far more fruitful than was my own in the Sierra Madre.

TABLE III

DIFFERENCES IN POPULATION DENSITIES OF CRYPTOPHILIC AND NOCTURNAL REPTILES IN DIFFERENT AREAS OF THE OAK-PINE ZONE

The figures are based upon the collecting success of Slevin (1939, 1942) and Stuart.

Species	Locality	
	Tecpán Region (Slevin) 30 Days	Sierra Madre (Stuart) 20 Days
Barisia moreleti subsp. ..	80	5
Rhadinaea godmani	6	4
Geophis rhodogaster	6	3
Tropidodipsas fischeri ..	12	3
Bothrops godmani	8	1
Total	112	16

Other conditions being equal, oak groves or mixed oak-pine usually support larger populations of reptiles than do stands of pure pine. Table IV is a summation of my collections of two saurian species in the oak-pine

TABLE IV

DIFFERENCES IN POPULATION DENSITIES OF *Anolis* AND *Sceloporus* IN TWO FOREST TYPES IN THE OAK-PINE ZONE OF THE SIERRA MADRE

The figures include the number of specimens observed in addition to those collected. The man-hours refer to the number of hours of observation.

Genus	Pine Forest			Oak-pine Forest		
	Number of Specimens	Man-hours	Density Index	Number of Specimens	Man-hours	Density Index
Anolis	0	12	0.00	25	45·7	0.55
Sceloporus	2	12	0.17	38	45·7	0.83
Total	2	12	0.17	63	45·7	1.38

zone in the Sierra Madre. The figures are based only on collecting in areas which were comparable in all environmental features other than cover and which undoubtedly approached natural conditions. Results obtained in such regions suggest that reptilian life in the oak-pine zone must have been exceedingly sparse in the primeval forest.

The loose ecologic relationship between environment and herpetofauna which characterizes the zoogeographic pattern in the oak-pine zone obtains also in the pine-cypress belt. In general, the pine-cypress zone has suffered less from the impact of human culture than has the oak-pine zone. Aside from corn along its lower limits, the land is suited only for potato growing and sheep grazing. Even though wood is cut from the forests, clearing has been much less intensive at the higher elevations than at the lower, where the greater part of the population of the southwestern highlands is settled. Conditions are, therefore, far more natural in the higher than in the lower zone.

The aquatic environment is but poorly developed in the pine-cypress belt. Rainfall is not heavy, and most of the precipitation is in the form of dense soaking mist, which is a characteristic feature of the region even during much of the dry season. As a result most of the higher zone is fairly well watered. Unlike the lower zone, however, the ponds are small and scattered and the lenitic habitat exists, for the most part, as small pools fed by adjacent springs or as quiet pools in the rivulets that flow through the area. These rivulets at the higher levels, except for occasional floods following heavy rains, flow quietly through mountain meadows in narrow channels, often only a few inches wide and even shallower in depth. On the flanks of ridges the streamlets merge to produce streams of fair size and considerable velocity.

Only two truly aquatic species occur in this zone, *Bufo bocourti* and *Plectrohyla cotzicensis*. *Bufo bocourti* is confined almost entirely to the pools adjacent to springs, and the eggs and tadpoles may be found in considerable numbers at almost any season of the year. In contrast, *Plectrohyla cotzicensis* is confined largely to the rivulets at high levels in which the gradients are less than those on the flanks of the mountain blocks. When such rivulets have their sources in spring-fed pools, *Plectrohyla* invades the pools and the tadpoles and young occur in considerable numbers late in the dry season (April). As might be expected, *Thamnophis eques fulvus* is not infrequent along the margins of such water holes.

Of the five strictly terrestrial species in the pine-cypress zone (*Abronia vasconcelosii* is too poorly known to be included among them), all have a marked preference for the open bunchgrass and short-grass plains rather than for the cold, damp forests that prevail. Their distribution here was more closely associated with major geographic lineaments than it was in the oak-pine zone.

Surprising as it may seem, *Pseudoeurycea rex* and *Magnadigita rostrata* were both far more abundant on the bunchgrass plains of the Sierra Madre than they were in the pine, cypress, or even in the scattered stands of oak. Similarly, in the María Tucum area between Los Encuentros and Totonicapán *Magnadigita rostrata* was more frequently observed beneath logs in openings along the edges of the pine forests than within the forests themselves. The reptiles, although *Barisia moreleti* subsp., *Sceloporus malachiticus smaragdinus,* and *Thamnophis eques fulvus* may be encountered in open pine forests, are all more common on the bunchgrass plains. As in the oak-pine zone, *Sceloporus malachiticus smaragdinus* is most frequent along rock-bordered streams and in rock fields, while *Barisia moreleti* subsp. seeks the cover offered by the dense tangle of the roots of the individual bunchgrass clumps. The occurrence of *Thamnophis eques fulvus* cannot be predicted. An illustration of the preference of the fauna for open areas was observed at Serchil. Three man-hours of collecting in a cypress forest yielded not a single specimen of *Sceloporus,* yet along a road cut through the same forest (Pl. IV, Fig. 2) the species was so abundant that no accurate count of the individuals could be made.

The pine forests seem to offer a more suitable environment for the herpetofauna than does the cypress forest. The pine forest with its open groves and often parklike appearance presents conditions tolerable to practically every species in the pine-cypress zone. The cypress forests, on the other hand, denser and wetter than the pine and with a much poorer living ground cover, is almost devoid of reptilian and amphibian life. In the Sierra Madre only *Pseudoeurycea rex* was secured in the cypress and in the Santa Elena region Schmidt (1936: 165) recorded a preponderance of the same species over *Magnadigita rostrata* in the same habitat.

In summation, it may be reiterated that the fauna of the southwestern highlands, although displaying surprising tolerance to local environmental factors within a single zone, is, nevertheless, sharply delimited vertically. This fact, I consider, holds the key to an explanation of the nature of the Plateau assemblage and its origin and history. But before these problems may be discussed, it is necessary to explain the factors which may have been or may be involved in controlling the major zoogeographic lineaments.

Of the eighteen forms which comprise the herpetofauna of the southwestern highlands (the two races of *Barisia moreleti* are considered as a single form), only four are common to the two zones, and only one of these, *Barisia moreleti fulva,* is endemic to the Chimaltenangan life area. This, together with the lack of any close faunal-environmental relationship insofar as major geographical lineaments within a single zone are concerned, indicates that the zoogeographic pattern on the southwestern highlands is controlled basically by some factor associated with altitude.

Vegetation, as a biotic expression of the sum of a number of environmental features, has often a close geographic coincidence with animal communities. It has already been demonstrated, however, that within the limits of a single zone, there is at best only very slight coincidence in the local distribution of the herpetofauna and vegetation. Although quite different when viewed *in toto,* the major cover types of the southwestern highlands, with the exception of the cypress forests, are represented in each of the two vertical belts. Both pine forests and open bunchgrass plains are extensively distributed throughout both the pine-cypress and oak-pine zones; and oak forests, though more commonly associated with lower elevations, do occur at very high levels (Serchil, 3000 m.). Cypress, however, is restricted to the upper zone. Insofar as vegetation is concerned, the majority of the species of the Chimaltenangan herpetofauna could encounter suitable habitats in either zone. This is particularly true of the oak-pine fauna. Only *Pseudoeurycea rex* of the pine-cypress fauna, which is possibly not restricted to, but is certainly most abundant in, that environment, might encounter unfavorable conditions of cover in the oak-pine belt. Since the oak forests of the pine-cypress belt are discontinuous in their extent and infrequent, there is a probability that *Magnadigita morio,* if it be restricted to the oak, has failed to become established at high levels.

Such related features of vegetation as light, density of stand, humidity, or abundance of ground litter may exercise geographic limitations on the fauna. Abundance of ground litter has a profound effect upon the local distribution of the cryptophiles, but could hardly be a limiting factor to the vertical extent of the oak-pine fauna, since litter is plentiful in the pine-cypress forests. Presence of litter could conceivably restrict such forms as *Pseudoeurycea rex* and *Magnadigita rostrata* to higher elevations, because it often occurs there in greater abundance and is generally wetter than that in the oak-pine belt. The humidity of the ground litter is more a function of climate than of vegetation and will be discussed later. Light might be a deciding factor in the distribution of the terrestrial phanerophiles, but only *Anolis crassulus crassulus* of this group is restricted vertically. That species is more of an open-country form than a forest inhabitant, and the higher levels would certainly present tolerable conditions of light. Density of stand constitutes a factor controlling both light and, to a lesser extent, humidity within the forests and is not, therefore, a vegetational feature directly associated with the distribution of any species. In summation, then, all available evidence suggests that, with the possible exception of *Magnadigita morio* and *Pseudoeurycea rex,* vegetation *per se* plays only a very minor role in limiting the vertical distribution of the herpetofauna of the southwestern highlands.

Of the several physical features of the environment which may control the zoogeographic pattern, physiographic forms, *per se* or in a secondary role, are suggestive as influences. As a generalization, two major types of land forms may be recognized in the region, the rolling uplands of moderate relief and the valley and plateau slopes of high relief. With the exception of *Sceloporus malachiticus smaragdinus,* which occurs throughout the southwestern highlands in the vicinity of rock outcrops, talus slopes, boulder-strewn flood plains, or the like, no correlation exists between the distribution of any Chimaltenangan species and any local physiographic feature. Possibly, however, the steep valley and plateau slopes, which support only a scanty ground cover at best, present something of a physical barrier to the free movement of cryptophilic species from one zone to another. Such a barrier, however, is always local and discontinuous in its extent.

It is as determiners of aquatic habitat types that physiographic forms appear to have their most important role. The lenitic habitat is but poorly developed in the pine-cypress zone, and on the steep slopes lying between the lower plains of the oak-pine zone and the high-level surfaces, standing water is a most unusual feature. That *Bufo bocourti* alone of the lenitic types of the oak-pine zone invades the pine-cypress belt certainly suggests that either the discontinuity of the lenitic habitat between the two zones or the actual sparsity of such an environment at high levels may be the controlling mechanism in the distribution of the lenitic types. *Bufo bocourti* with its high tolerance to terrestrial conditions has probably been able to transcend the slope barrier and to become established in a relatively unfavorable region, where the less terrestrially tolerant species, *Hypopachus barberi* and especially *Rana pipiens,* have failed.

No such case can be established for the lotic species. This group, which includes *Plectrohyla cotzicensis, Plectrohyla guatemalensis,* and *Rana macroglossa,* is tolerant to almost unbelievably severe lotic conditions. Such features as falls, decrease in volume during the dry season, or the intensive molar action of the load carried during flood periods have not dislodged them from the swift mountain rivulets in which they live, nor could they conceivably have acted as a barrier to their free movement from one zone to another.

I believe that climatic factors have been and still are responsible for the geographic limits of the majority of the species occurring on the southwestern highlands and that they have probably been largely instrumental in determining the very nature of the Plateau assemblage as a whole. It has previously been indicated that there is an inverse correlation not only between altitude and temperature but between altitude and precipitation as well. Nevertheless, atmospheric humidity and decreased evaporation undoubtedly produce a wetter environment in the pine-cypress zone than in the oak-pine belt.

Above the sharp climatic (*A–C* boundary of Köppen), faunal (Schmidt, 1936), and cultural (McBryde, 1947) breaks so conspicuous in the neighborhood of the 1500 m. contour, all changes are more gradual. Temperature is gradually reduced from *Cb* conditions through *Cc* and into *E* at the higher levels. The oak-pine zone changes just as gradually over to the pine-cypress, and faunal and cultural transitions occur just as gradually in the relatively broad region between 2600–3000m. Nevertheless, the cold, raw, fog-soaked pine-cypress zone is distinct from the dryer and milder oak-pine belt.

Of the phanerophiles of the southwestern highlands, *Anolis crassulus crassulus* and *Bothrops godmani* are restricted to a single belt, the oak-pine. In view of the tolerance of the former species to environmental variables within that zone and the extensive range of the latter, it seems reasonable to assume that temperature alone may be the factor limiting their vertical extent. Among the cryptophiles restricted to the oak-pine zone, *Tropidodipsas fischeri, Rhadinaea godmani,* and *Geophis rhodogaster* appear to present cases comparable to that of the phanerophiles. An assumption that temperature is a limiting factor in the distribution of the salamanders cannot be well supported.

Among the aquatics, *Rana pipiens* and *Hypopachus barberi,* restricted to the oak-pine, could conceivably have been delimited by temperature in their vertical distribution, but discontinuity in the lenitic environment would seem to be a more logical explanation. Though it might well be unable to withstand competition from *Plectrohyla guatemalensis* in the oak-pine zone, no physical factor of the environment other than intolerance to higher temperatures appears to account for the absence of *Plectrohyla cotzicensis* from the oak-pine belt. Conversely, it seems fairly logical to assume that reduced temperatures in the pine-cypress zone restrict the lotics *Rana macroglossa* and *Plectrohyla guatemalensis* to lower levels. Thus, it is possible that temperature is a limiting factor to the vertical extent of eight and possibly ten of the thirteen species of reptiles and amphibians which are restricted to a single vertical zone on the southwestern highlands.

Aside from the true aquatics, only the salamanders of the herpetofauna are intolerant to xeric conditions, so that humidity, either as rainfall or in atmospheric form, does not seem to play an important part in the determination of vertical limits. *Magnadigita morio* is closely associated with oak cover, which is poorly developed in the pine-cypress zone, but both *Pseudoeurycea rex* and *Magnadigita rostrata* show no such environmental specificity. It is conceivable that the dryer conditions of the ground litter in the oak-pine zone, especially during the dry season, may be the environmental factor which accounts for the absence of these two species from that zone. It is not improbable, however, that temperature alone or in combination with humidity may be the determiner.

An environmental feature varying with altitude which may be of some importance in delimiting the vertical extent of the herpetofauna is oxygen pressure. I have some data, not yet ready for publication in complete form, which seem to indicate that oxygen pressure may play a more than minor role in the vertical distribution of reptiles and amphibians. In comparing the hemoglobin values of the lowland *Bufo marinus* with those of the upland *Bufo bocourti,* it was found that the blood of *bocourti* carries a mean of 22 per cent more hemoglobin per unit volume of blood than does that of *marinus.* There is, however, no significant difference in the hemoglobin value of the blood of populations of *Bufo bocourti* living at elevations ranging from 2200 to 3200 m. This would seem to indicate that even though oxygen pressure might be of some importance in delimiting the upper extent of lowlanders, highland species are adjusted physiologically to the extreme condition of reduced oxygen pressure encountered within their vertical range.

Thus, the vertical limits of the several species of which the herpetofauna of the southwestern highlands is composed are probably determined in a large measure by temperature. Some evidence, however, indicates that humidity and, occasionally, physiographic forms or vegetation types may play an active role in producing vertical zoogeographic lineaments.

CONCLUSIONS

Earlier in this paper it was intimated that a knowledge of the local distribution of the Plateau assemblage in a typical highland habitat might supply data upon which could be based some general conclusions concerning the origin of that assemblage and the history of its development, and might throw some light as well on the role of the highlands of northern Central America in determining the nature of herpetofaunal agglomerations to the north and south. Though there are insufficient data to treat of any of these problems with conclusiveness, an analysis of the foregoing data is sufficiently suggestive to warrant consideration.

History of the Plateau Herpetofauna

In essaying an account of the history of the Plateau assemblage, several questions, aside from the strictly historical aspects of the fauna, may be posed. From what sources have the components of the assemblage been derived? Why is the assemblage composed almost entirely of well-differentiated highland groups? Why has it received so few immigrants from the adjacent lowlands? Why has it remained so impoverished? Why has it undergone such extensive local differentiation within the highlands? These and other questions find their answers in the historical and ecological aspects of the herpetofauna and in the nature and history of the environment now occupied by that assemblage.

The fauna may be analyzed with respect to its historical relationships. In discussing the origin of the herpetofauna of Alta Verapaz in a recent paper (Stuart, 1950), it was concluded that the herpetofauna of northern Central America as a whole is composed of the following elements:

- Autochthonous Middle American element (Stuart, 1950)
- Old Northern element (Dunn, 1931)
  - Older element
  - Younger element
- South American element (Dunn, 1931, in part)

The Plateau assemblage contains representatives from the first two categories only, and the various genera represented in that assemblage may be arranged as follows:

AUTOCHTHONOUS MIDDLE AMERICAN
Plectrohyla
Anolis
Sceloporus
Rhadinaea
Geophis
Tropidodipsas

OLD NORTHERN
Magnadigita (older)
Pseudoeurycea (older)
Bufo (older)
Rana (older)
Hypopachus (older)
Abronia (younger?)
Barisia (younger?)
Thamnophis (younger)
Bothrops (older)

No South American element is included in the Plateau assemblage. Certain forms such as of the genus *Xenosaurus* or the *veraepacis* group of *Adelphicos,* both of fairly ancient ancestory, have not attained a place in the Plateau assemblage, though they are typically upland types in northern Central America. Moreover, several widespread genera, *Geophis, Bufo,* the gerrhonotids, and *Thamnophis,* which have invaded highland areas in regions not too far distant from northern Middle America are at best only poorly represented in the Plateau assemblage. The importance of these observations will be made apparent later.

The history of the area occupied by the Plateau assemblage has not been particularly complex. It is generally agreed by geologists that "nuclear Central America" was, prior to the Pliocene orogeny, an upland mass of moderate elevation. From mid-Eocene until mid-Miocene or possibly even early Pliocene this region was isolated from South America by various open portals between Nicaragua and Colombia. During that time northern Central America extended southward from the main block of North America as a peninsula. Later, during late Miocene and perhaps into early Pliocene this mass, though in contact with South America, may have been separated from North America owing to an open portal in the Tehuantepec region.

Until the Pliocene a warm, moist climate with tropical forest and forest margin conditions probably prevailed over most of the region (Olsen and McGrew, 1941). With the onset of the Pliocene, however, the temperature of the extant highland region began dropping owing especially to the elevation of the area by the great Pliocene orogeny. To what extent northern Central America was further cooled during Pleistocene glaciation can only be surmised. Flint (1947: 455–56) estimated temperature reductions of from 4° to 8°C. for various parts of the globe, and Griscom (1932) suggested that a reduction of some 7°C. in the temperature of Central America, accompanied by the descent to sea level of a subtropical zone, took place. So great a temperature reduction seems to me unlikely and certainly not in keeping with the evidence presented by the extant herpetofauna of northern Central America. First, in this narrow isthmian region, one might expect temperature reduction to be tempered by adjacent marine conditions. Second, descent to sea level of a subtropical zone would have brought about either widespread extermination of the tropical fauna or acclimatization of that fauna to subtropical conditions. That extermination did not occur is evidenced by the survival of many Old Northern types on the lowlands, notably the turtles, several groups of oedipi, skinks, colubrids, and micrurids. Had acclimatization taken place, a host of forms would certainly have been able to invade high elevations once extant climates had developed, a condition which it is known did not take place. The evidence, therefore, points to the presence of a tropical environment in northern Central America even at the height of Pleistocene glaciation.

Schmidt (1943) and Dunn (1931) have shown that Central America was, through the Cenozoic period, invaded by successive herpetofaunal waves from both the north and the south. The first of these waves swept in from the north sometime prior to the mid-Eocene. The greater part of the first wave moved southward into South America, where, during the isolation of that continent, it developed into the South American element (*sensu* Dunn). Another part, however, remained stranded in Middle America, so that the prototypes of a number of modern genera were apparently represented on both sides of the open southern Central American portal during much of the Cenozoic. This stranded element in the north was to give rise to the Autochthonous Middle American element (*sensu* Stuart). On the heels of the first wave came a second, the older Old Northern group (*sensu* Dunn). It reached Middle America too late to permit its entrance into South America, owing to the open portal in the south. There were present then, on what Schmidt (1943) has called the "Central American paleopeninsula" and the Mexican Plateau, after the mid-Eocene, two major assemblages of reptiles and amphibians of different phylogenetic relationships and origins, undergoing similar histories. Though the prototypes of certain extant groups were probably widespread through the ancient Mexican–northern Central American peninsula, it is indicated that others were restricted either to the Mexican section (north of the modern Isthmus of Tehuantepec) or to the Central American section (south of the modern Isthmus of Tehuantepec). Among the ancient iguanids, the prototype of *Sceloporus* was probably represented only in the north, and that of *Anolis* was apparently restricted to the south.

With the closing of the portal in southern Central America, the invasion of Middle America by the well-developed South America element got under way. Apparently, before any of these invaders had become sufficiently adapted to enter the uplands of nuclear Central America, the Pliocene orogeny had been initiated, thus producing on those rising highlands climatic conditions too severe to permit the southern thermophiles (heat lovers) to spread into them.

As the uplands rose, some representatives of the Autochthonous Middle American and Old Northern elements underwent further differentiation and split into highland and lowland groups, as, for example, the *inguinalis* and *cuneus* groups of *Hypopachus,* respectively.

In the meantime further invasion from the north had probably ceased owing to the opening of the Tehuantepec portal, but with the closing of that portal in late Miocene or early Pliocene conditions other than climatic were such as to set the stage for a fourth faunal invasion of the region. This wave included some of the younger Old Northerners as well as Authochthonous Middle Americans, such as *Pseudoeurycea* and *Sceloporus,* respectively, that had been developing during the Cenozoic on the Mexican section of the Middle American peninsula, together with groups of somewhat less ancient ancestry that had evolved in the same region, such as *Thamnophis.* The fourth wave, probably composed of psuchrophiles (cold lovers), presumably had to await world refrigeration to enable it to move southward from the Mexican uplands. In addition to the genera just noted, *Abronia* and *Barisia* appear to have been included in the southward movement of this wave. The components of the group, incidentally, belonged to the younger Old Northerners (*sensu* Dunn). Tihen (1949*b*) suggested a somewhat earlier movement southward by the gerrhonotids, but this seems hardly necessary to account for their evolution or extant distribution and is certainly contrary to what might be expected of a predominantly xeric highland group. It is indicated, nevertheless, that *Abronia* has experienced a somewhat longer residence in Central America than has *Barisia.*

Concurrent with this new invasion, the environmental conditions now associated with higher elevations in northern Central America were probably present at relatively low levels, so that there must have existed somewhat greater continuity in the pine-cypress zone, for example, than there is now. The present-day wide distribution of species which occupy environments now discontinuously distributed over the highlands of northern Central America could not otherwise be accounted for without resorting to improbable theories of widespread polyphyletic origin and subsequent convergent evolution. Whatever the explanation, the highlanders must have been by this time sufficiently well differentiated from the lowlanders to have permitted the two groups to retain their identities during the glacial period.

As the extant climates began their development with the retreat of the Wisconsin ice sheet, the highland assemblage apparently followed the migrating cooler climates into higher and higher elevations. At this time local isolation on the highlands of northern Central America was probably initiated, since there was no longer areal continuity in the several environments. As a result, local faunas now underwent differentiation enhanced by this isolation and separated by barriers either of a geomorphologic or climatic nature. It is not improbable, however, that local differentiation had been initiated in the Old Northern and Autochthonous Middle American cryptophiles prior to this time.

This historical summary, though essaying an account of the history of the Plateau assemblage, leaves several of the questions previously posed still unanswered. Of especial significance is the impoverishment of the assemblage. A number of groups represented at high elevations in adjacent regions are either absent or at best poorly represented in the Plateau assemblage. Among the forms which are essentially lowlanders and might be expected to have supplied at least one representative to the assemblage are *Eleutherodactylus, Hyla,* and *Dryadophis,* while others, such as *Bufo, Anolis,* and *Bothrops,* have provided the assemblage with but a single form each. Groups which are essentially highlanders in Central America, or at least are well represented on the Mexican Plateau but which fail to participate or are barely represented in the Plateau assemblage, include *Chiropterotriton, Pseudoeurycea, Xenosaurus, Sceloporus,* and *Adelphicos* (*veraepacis* group).

Gadow (1905 and 1910) stressed the multitudinal factors involved in "altitude" and its effects upon the herpetofauna of Mexico, but in dealing with the herpetofauna of the plateaus of northern Central America, "altitude," aside from the inference of reduction in temperature and oxygen pressure, carries no particular connotation. It is better to disregard the catch-all factor of altitude and examine some of the more important individual factors which were perhaps responsible for the impoverishment of the Plateau assemblage.

The very approaches to the plateau have not enhanced the ease of its invasion by many groups. Over most of its extent on both the north and the south it is fairly effectively isolated from the lowlands by steep, barranca-cut walls, and approach from the east and west along gentler slopes may be accomplished only by way of subhumid environments. On either approach the lenitic environment is but poorly developed, and this has certainly been a great factor in eliminating any possible chance of invasion of the region by many of the lowland amphibians which are essentially pond forms. With the sparsity and discontinuity of the lenitic environment on the highlands themselves this has undoubtedly been a factor in limiting the number of lenitic types in the area.

With reference to climatic factors, the importance of temperature in delimiting the vertical extent of the various components of the Plateau assemblage themselves has already been suggested. In much the same way it may well have been of prime importance in delimiting the size of the Plateau assemblage. Several lotic hylas that occur on the escarpment slopes give evidence of being restricted to lower elevations by temperature alone, and it certainly cannot be ignored in the case of many other groups, especially those of southern origin. Insofar as northern types have been concerned, there seems to be no good explanation for their not having invaded the Central American plateaus during the Pleistocene, when a relatively cool environment must certainly have formed a bridge between the Mexican Plateau and the highlands to the south across the relatively low Isthmus of Tehuantepec. Certainly such forms as *Barisia* and *Sceloporus malachiticus* give evidence of having entered Central America along that route. It may have been that some groups descended to the lowlands proper and became adapted to megathermal and mesic conditions and that a subsequent adjustment to microthermal and more xeric environments has been impossible. Gadow many years ago noted (1905: 239) that "it seems easier for xerophile northern genera, and even species, to go south and to adapt themselves to life in a more equable, hot and decidedly moister country with luxurious vegetation, than for hygrophile southerners to do the reverse."

Humidity, especially appears to have played more than a passing role in restricting the size of the Plateau assemblage. The pine-cypress zone constitutes one of the most humid environments in Central America, but this is separated from the humid lowlands by the relatively subhumid oak-pine zone, which would certainly have proven intolerable to many hygrophiles. This is certainly true insofar as much of the leaf-mold fauna of the very humid Pacific versant is concerned.

The uniformity of vegetational cover in the highlands and the absence or at least sparsity of such plant groups as the bromeliads may well have prevented the invasion of the highlands by additional groups. There can be little doubt that bromeliad salamanders, and hylids known from annectent regions, have failed to enter the region because of the sparsity and discontinuity of their highly specific habitats.

Furthermore, the lack of diversity in the highland environment as a whole has apparently restricted the size of its herpetofauna. It seems probable that this lack of environmetal diversity has been a barrier to the invasion of the highlands by many groups, even when other environmental factors would have made invasion possible. It would have been difficult for many species to have survived competition from groups already established in the relatively few ecologic niches available on the highlands.

Finally, aside from these specific factors, the highlands present an environment which not only is at best inclement to amphibians and reptiles and lacking in diversity, but has also suffered from the impact of relatively recent climatic changes and geomorphological disturbances.

If all these various factors be considered as a unit rather than individually, it is not surprising that the plateaus of Northern Central America, despite their antiquity, have proven relatively unsuitable as an environment for amphibians and reptiles. The few forms which have managed to gain a foothold in the region are mostly those which presumably evolved with the environment and a handful of more recent immigrants that have apparently been possessed of a high degree of either tolerance or plasticity.

Differentiation Process in the Plateau Herpetofauna

Though the process of differentiation in the Plateau herpetofauna has been treated in a general way in the preceding historical account, there are certain features which warrant further consideration and which may, when analyzed, be of some general biological interest.

It is important to emphasize that the Plateau assemblage is made up of forms which, during their histories on the plateaus of northern Central America, have differentiated from their relatives in adjacent areas to degrees varying from the generic down to the subspecific level. In making use of these observations on the several levels of differentiation, it is important to realize that one may or may not be dealing with real differences. Only within the limits of a single genus can one measure with any accuracy the amount of differentiation. In dealing with several genera the measurement becomes less accurate and in comparing different classes, as in handling an entire herpetofauna, many factors must be considered in analyzing apparent differentiation levels. A particular source of error lies in the subjective nature of the generic concept. In an instance at hand, *Magnadigita* and *Pseudoeurycea* constitute valid genera in the minds of some systematists, but others consider them no more than species-groups within the limits of an all-encompassing genus *Bolitoglossa* (s.l.).

Again it is difficult to compare the amount of differentiation in diverse groups. One may well ask whether *Bothrops godmani* has diverged as far from the lowland members of the genus as have *Magnadigita, Plectrohyla,* or the *godmani* group of *Rhadinaea* from their relatives in other regions. Without a common denominator upon which to erect systematic categories above the specific level, or some factor which will serve as a basic constant from which to estimate divergence in diverse groups, evaluation of the amount of differentiation cannot be dogmatic.

It is, nevertheless, fairly apparent that differentiation from relatives in adjacent regions is greatest in those members of the assemblage autochthonous to Central America and least in those that are more recent entrants from the north, that is, such as *Magnadigita, Plectrohyla, Rhadinaea* vs.

Pseudoeurycea rex, Sceloporus malachiticus, and *Thamnophis eques fulvus.* On the other hand there appears to be neither rhyme nor reason in the level to which local differentiation has taken place within the highland areas. For instance, *Magnadigita* has specific representatives in each of the several life areas, but *Barisia* has differentiated locally only to the subspecific level, and there is no local differentiation in *Bothrops godmani.*

As noted by Simpson (in Jepsen, Mayr, and Simpson, 1949: 225), one has come to accept as axiomatic a direct correlation between tectonic disturbances and evolutionary rates despite the fact that very little data on the subject has been either gathered or properly evaluated. Upon examining the differentiation levels in the Plateau assemblage in the light not only of tectonic disturbances but of general events in the environmental history of Middle America, some correlations are encountered that seem suggestive. Four major environmental events, which took place in the course of the Cenozoic history of Middle America, may have been especially pertinent. The first was the open portal from mid-Eocene through the Miocene in southern Central America thus isolating, one from the other, the two closely related groups on either side of the break. The second was the great Pliocene orogeny. The third was the world refrigeration that accompanied the Pleistocene. And the fourth was the return of equable climates following the retreat of the Wisconsin ice sheet.

It is my belief that the impact of these four events upon the herpetofauna may very well explain the several differentiation levels now observed in the Plateau assemblage. The open portal in the south permitted the Autochthonous Middle American fauna to evolve during the mid-Eocene-Miocene interval. During that period it seems fairly certain that such genera as *Bolitoglossa* (s.l.), *Plectrohyla, Hypopachus, Tropidodipsas, Rhadinaea,* and *Bothrops* developed in the Central American region. Certainly, it would almost have to follow that the generic characters of these groups had to be well established before any split between the highland and lowland groups in those genera could have taken place.

The Pliocene orogeny seems to have been the only event that could have provided the environmental impact necessary to split off the highlanders from the lowlanders. During that period the representatives of those groups in the several genera must have undergone sufficient differentiation one from the other to have permitted them to retain their identities during the Pleistocene, when the highlanders were undoubtedly "crowded" into lower elevations and brought into close proximity with the lowlanders. It may be suggested, therefore, that differentiation to some "subgeneric" level must have occupied most of the Pliocene, when such groups as *Magnadigita,* the *inguinalis* group of *Hypopachus,* the *fischeri* group of *Tropidodipsas,* the *godmani* group of *Rhadinaea,* and *Bothrops godmani* presumably came into being on the highlands of northern Central

America. There may have been an open portal in the Tehuantepec region during this same time, that enhanced differentiation on either side of that break, as seems indicated by the occurrence in northern Central America of such groups as *Magnadigita, Rhadinaea decorata,* and *Micrurus affinis* and *nigrofasciatus,* all essentially represented by other groups to the north of the Isthmus.

The main effect of Pleistocene cooling on the Plateau assemblage seems to have been to have permitted the southward migration of certain groups from the Mexican Plateau region. It is further possible that among the well-established highlanders some local differentiation may have been initiated at this same time, but all differentiation above the species-group level had probably been completed by this time insofar as highlanders and lowlanders were concerned. Further differentiation in the Plateau assemblage from then on was local within the limits of the Plateau area.

Local differentiation in the Plateau assemblage extends from the specific level down to an absence of local differentiation. The differentiation appears to have been caused or directed by two groups of factors. Internal factors of the organism of major importance are the mobility of the organism, the nature of its habits, whether cryptophile or phanerophile, and its tolerance to the varied features of its environment. Though mutation is an important factor, nothing is known of its rate in the fauna under consideration. It is, accordingly, necessary to treat the mutation rate as a constant. Among the external factors of the environment the most important has been the shifting of highland environments from lower levels to higher ones with the retreat of the Wisconsin ice sheet, thus causing local barriers to develop between the several very high blocks which make up the plateaus. The headwater valleys of Río Negro and Río Saleguá and the gorge of the lower Río Negro, all relatively low and possessed of subhumid climates, are of particular importance as isolating mechanisms insofar as the southwestern highlands, the Cuchumatán Mountains, and uplands of Alta Verapaz, respectively, are concerned.

Of the internal factors, the habits of the several organisms exhibit a direct correlation between secretiveness and degree of differentiation. If the Autochthonous Middle American and older Old Northern reptiles are arranged according to their degree of secretiveness from greater to lesser, the following line results: *Geophis, Rhadinaea, Tropidodipsas, Anolis, Bothrops* (nocturnal).

Geophis may be eliminated as barely represented in the Plateau assemblage. Of the others, it may be noted that *Rhadinaea* has differentiated to a specific level in the southwestern highlands, Cuchumatán Mountains, and Alta Verapaz; that *Tropidodipsas* is possessed of but two species, one in the southwestern highlands and the Cuchumatán Mountains and the other in the Alta Verapaz (*Anolis crassulus* has undergone but subspecific differentiation in those same two areas), and finally, that *Bothrops godmani* has remained undifferentiated throughout the highland area. The same correlation obtains among the more recent entrants from the north, that is, *Barisia, Sceloporus,* and *Thamnophis,* respectively, except that differentiation begins at the subspecific level in *Barisia.*

Of the external factors, the xeric river valleys between the several mountain blocks that go to make up the plateaus, are isolating mechanisms of varying degrees of efficiency, depending upon the mobility of the organism and its tolerance to subhumid conditions or to other conditions that depart from the optimum. *Magnadigita* is a group of organisms that not only has weak powers of movement, but greater water requirements besides. As a result there is specific differentiation in the *dunni* group of the genus in the Cuchumatán Mountains, the southwestern highlands, and the Alta Verapaz. The *morio* group has differentiated to the specific level in only the first two regions and does not occur in the Alta Verapaz. It is entirely possible that the extreme aridity of the Río Negro gorge as well as its very low elevation in the region between the Cuchumatán Mountains and Alta Verapaz has been a barrier too great to be transcended by *morio* and several other groups. Certainly in that area the valley is a far more formidable barrier than in the headwater regions.

Among the lotic types, *Plectrohyla,* like *Magnadigita,* has undergone differentiation to the specific level in several life areas. It is restricted essentially to mountain freshets at relatively high elevations and the several populations of the genus have apparently been isolated one from the other since the retreat of the Wisconsin ice sheet. *Rana macroglossa* not only descends to much lower elevations than does *Plectrohyla,* but it also tolerates conditions existing in a greater variety of running waters. Consequently, it has remained undifferentiated in the various subdivisions of the highlands of Northern Central America. Among lenitic types *Hypopachus* has, like *Plectrohyla,* differentiated to the specific level in several regions. In contrast the more terrestrial *Bufo bocourti* has remained undifferentiated throughout the highlands. It is interesting that, despite its tolerance, *Bufo bocourti* does not occur in the Alta Verapaz. This is probably because in that region there is a dearth of breeding sites at elevations at which the species lives. Local differentiation in the Plateau assemblage, therefore, appears to have been a fairly recent process, which is assumed to have been made possible through the development of local barriers acting as isolating mechanisms with varying efficiency depending upon the nature of the organism. Though possibly initiated in the early stages of the Pleistocene in such sedentary types as *Magnadigita,* where distance would permit various populations to drift genetically in different directions, complete differentiation apparently awaited the elevation of the oak-pine and pine-cypress zones, when local barriers of relatively low elevations developed to isolate the several populations.

From these observations one may see that the rate of differentiation in the diverse groups that go to make up the Plateau assemblage has been anything but uniform and that the rate is dependent upon a number of factors. Nevertheless, insofar as the most rapid rates of differentiation are concerned, the above data are suggestive. They indicate that differentiation to the generic level probably occupied the interval between the mid-Eocene and the end of the Miocene, when such genera as *Bolitoglossa* (s.l.), *Plectrohyla, Rhadinaea, Tropidodipsas,* and *Bothrops* are presumed to have taken form. Subgeneric differentiation appears to have been accomplished during the Pliocene, as seen in the questionable genus *Magnadigita,* the *godmani* group of *Rhadinaea,* the *fischeri* group of *Tropidodipsas,* and *Bothrops godmani.* Specific differentiation is believed to have been accomplished since the onset of the Pleistocene in such forms as the several species of *Magnadigita* and in *Rhadinaea.* Subspecific differentiation has apparently been attained since the retreat of the Wisconsin ice sheet in a few instances, as in *Sceloporus malachiticus* subsp. and *Barisia moreleti* subsp.

As to the nature of local differentiation in the Plateau assemblage, it has been suggested in previous papers that there is evidence to support the assumption that it has been rectilinear (Stuart, 1942*d*: 179; Stuart and Bailey, 1941: 6–9). A reconsideration of the Plateau assemblage, however, in the light of more complete data than were formerly at hand, leads me to believe that differentiation in this herpetofauna has been largely nondirectional. Examination of the various morphological characters displayed by the several species and subspecies in the various areas definitely shows that with the possible exception of the *godmani* group of *Rhadinaea,* differentiation has been accomplished *in situ* from formerly more widespread prototypes, perhaps through random genetic recombinations operating in the presence of barriers. Furthermore, there appears to have been no apparent differentiation in the physiology and psychology of the various local species and subspecies. In only a single instance has there been deviation in the habits or habitats of any of the local forms within a single group. That deviation is *Magnadigita rostrata,* a species of an essentially bromeliad-inhabiting group which has descended to the ground and become entirely terrestrial.

Finally, though without experimental evidence, some data indicate that much of the local taxonomic differentiation in the Plateau assemblage has not been adaptive. As an extreme example, the various races of *Barisia moreleti* may be cited. These races differ one from the other primarily in the nature of contact between one or two superficial head scales that are literally plastered to the surface of a skull composed of very solidly ankylosed bones. Stern (in Jepsen, Mayr, and Simpson, 1949: 13–22) recently commented on the multiple-effects of genes and the possible physiological implications of a mutation of apparent minor morphological significance. It seems improbable, however, that, in the subspecies of *Barisia moreleti,* any physiological or psychological feature of survival value is associated with those mutations that express themselves in superficial morphological changes.

First, it will be observed that the various races of *Barisia moreleti* are differentiated one from the other largely through average differences, and individuals more or less typical of any race may occur within the population of any other race. This is particularly true of variants within the limits of *Barisia moreleti fulva.* This suggests that any race could survive within the limits of any other race. Secondly, it is difficult to conceive of any physiological character associated with these minor morphological differences as being of any survival significance in the face of the tremendous tolerance displayed by each race. *Barisia moreleti fulva,* for instance, has been captured in such diverse environments as in the wet cloud forest of the Pacific versant at 1700 m., on dry oak hillsides at 2500 m., on grassy slopes of pine parklands at the same elevation, and on the bunchgrass plains of the cold, wet, pine-cypress forests of the Santa Elena region at 3100 m. Finally, both *Barisia m. moreleti* and *m. fulva* survive equally well in the widely separated cloud forests of the Alta Verapaz and of the Pacific versant, respectively. These two environments are superficially identical, though it is possible that microclimatically they may not be uniform. Similar observations obtain in other genera, notably *Hypopachus, Plectrohyla, Anolis,* and *Sceloporus.*

Zoogeographic Role of the Highlands of Northern Central America

In a recent paper Smith (1949: 222–24) attached considerable importance to the Guatemalan Plateau as a herpetofaunal center of origin and dispersal. Although defining it broadly as a unit of the entire highland mass extending from Nicaragua northward to include the Mexican plateaus, he assigned to it more than passing importance as a center *per se.* Unfortunately, Smith does not differentiate between the moderately elevated uplands of northern Central America of pre-Pliocene times and the very high plateau that developed during the Pliocene. I have already appraised the importance of the pre-Pliocene uplands to the Middle American herpetofauna, and have intimated the magnitude of their role in relation to the zoogeography of the continental areas to the north and south. In the high plateau of Pliocene origin a different situation exists.

As previously noted, Pliocene elevation merely divided some of the more tolerant genera that had evolved in Central America into highland and lowland groups, but the great majority of the genera then present in northern Central America remained lowlanders. Subsequent dispersal of the highlanders merely extended the ranges of these few along highland routes into other highland areas. At most, the Guatemalan section of the more recent northern Central American highlands served as a center of origin and dispersal for only a very small and highly specialized fauna.

Moreover, these same highlands acted as something of a barrier to the free movement of various herpetofaunal elements toward the north and south through Central America since the Pliocene. In presenting an environment of both high relief and high elevation with extensive areas of subhumid climatic conditions, it is entirely possible that many groups which had evolved on the Mexican Plateau encountered in this region intolerable environmental conditions that blocked their southward movement along the highland route even after a crossing of the Isthmus of Tehuantepec had been effected during the early Pleistocene. Other groups that might have moved southward along mesic slopes at intermediate elevations would have encountered only very narrow pathways discontinuously distributed along those slopes. In moving northward, groups that may have evolved on the highland areas of southern Central America, would have encountered environmental conditions which had no extensive counterparts in the south, such as oak-pine forests and subhumid climatic conditions.

Furthermore, in rising to its present height the Guatemalan Plateau all but eliminated the surrounding lowlands. "Tropical Zone" environments persist along the Pacific as only a narrow band 40 kilometers wide, and along the Caribbean in the Guatemalan-Honduranian border region the highlands rise almost from the sea. In such restricted quarters lowland emmigrants from the north and south may have found movement toward the south and north, respectively, difficult, especially when they encountered firmly entrenched residents of some antiquity in the region. It seems probable that the extant highlands of northern Central America have, since the Pliocene, actually retarded both differentiation and movement in and through the isthmian region.

SUMMARY

The Plateau herpetologic assemblage in northern Central America is one of three distinct faunal agglomerations in the northern part of the isthmian region. In addition to the Plateau assemblage, there is present on the lowlands the Pacific assemblage along the Pacific and the Caribbean assemblage on the Caribbean side.

The Plateau assemblage is made up of fifteen genera and seventeen specific or supraspecific groups. It is an impoverished agglomeration of species and subspecies of reptiles and amphibians of Old Northern or Old Northern-like history largely endemic to the highlands of northern Central America, which has for the most part originated *in situ*.

On the southwestern highlands of Guatemala the Plateau assemblage is the predominant herpetological element, and only a few forms of other assemblages have invaded the region along its fringes.

The southwestern highlands are geologically a distinct mountain block overlain with igneous extrusions and volcanic deposits, which have been deeply dissected to produce a rugged upland varying from 1800 to 3700 m. in elevation. Climatically, the region is characterized by moderate to low temperatures, depending on the elevation; by subhumid conditions at elevations up to 2700 m.; and, owing to fogs and reduced evaporation, by excessively humid conditions above that level. Two major vegetational belts may be recognized in the region, the oak-pine below 2700 m. and the pine-cypress-bunchgrass above that elevation.

The herpetofauna of the southwestern highlands is composed of twenty-four species and subspecies of which only nineteen are considered true members of the fauna. The remaining five forms enter the highlands only along its borderlands. Nine of the forms are endemic to the southwestern highlands.

This group of forms constitutes a faunal entity which serves to characterize the southwestern highlands or Chimaltenangan faunal area.

Within the southwestern highlands, the herpetofauna is arranged into two faunal units, the limits of which are roughly coincidental with those of the two vegetational belts. The local distribution of the several species is shown to be correlated less with local environmental complexes than with their habits. Vertical limits appear to be controlled primarily by a temperature factor and to a lesser extent by such conditions as humidity, vegetation type, and geomorphological forms.

It is concluded that the impact of the Pliocene orogeny was mainly responsible for the origin of the Plateau assemblage, which appears to have evolved *in situ* on the newly formed highlands from essentially lowland genera that had developed in Central America during the mid-Eocene to Miocene interval. A few Pleistocene immigrants from the Mexican plateaus are the only exceptions.

The Plateau assemblage has remained relatively impoverished owing to the inclemency of the varied environmental factors that were produced primarily by the Pliocene orogeny.

Generic, subgeneric, specific, and subspecific levels of differentiation may have been attained during the mid-Eocene to Miocene interval, during the Pliocene, since the onset of the Pleistocene, and since the retreat of the Wisconsin ice sheets, respectively.

Differences in amount of local differentiation in the Plateau assemblage appear to be correlated more with the nature of the habits of the organisms than with the presence or absence of physical barriers.

Local differentiation in the Plateau assemblage appears to be, for the most part, neither rectilinear nor specifically adaptive.

The plateau of northern Central America has not been a center of either origin or dispersal of more than minor importance but has, rather, proved to be a barrier of major importance to the free movement northward and southward of not only lowlanders but of highlanders as well.

APPENDIX I

LIST OF COLLECTING LOCALITIES

The sites from which the bulk of the herpetological material from the southwestern highlands has stemmed and the itineraries of the collectors of that material have for the most part been well described. Godman (1915) has given an account of the assembling of the material described in the *Biologia Centrali-Americana,* Vaillant (1908) has published the itinerary of the *Mission scientifique au Mexique,* and both Slevin (1939) and Schmidt (1936) have noted the sites which they studied more recently. During his ornithological explorations in Guatemala, A. W. Anthony secured a few highland species, which are now in the Museum of Comparative Zoology of Harvard College. An account of his travels was published by Griscom (1932). In addition to these collections and my own, occasional specimens of highland species are scattered throughout America and European museums; most of these specimens carry incomplete data. It does not seem out of place, therefore, to include herein a complete list of the stations which have been visited for the purpose of collecting herpetological material on the southwestern highlands. All the localities given are either on the Guatemalan sheets of the American Geographical Society's map of Hispanic America or on Map 2.

Material which I collected and deposited in the collections of the Museum of Zoology, University of Michigan, was secured during the course of three field seasons in Guatemala. In 1944 I made a short trip over the southwestern highlands and stopped briefly at Panajachel. There and on María Tucum I secured a few specimens, but no systematic studies in the region were essayed.

The bulk of my material was secured during the season of 1947. I initiated my studies at Panajachel in mid-March and from there, at the end of the same month, I proceeded to Tejutla, where I remained during the first week in April, after which I crossed the Sierra Madre, staying until mid-April, at Tacaná. I visited briefly the arid Cuilco Valley, which marks the northern boundry of the Sierra Madre, before going on to Ixchiguán late in April. The month of May was devoted to carrying on investigations along the Pacific versant, after which I returned to Ixchiguán in early June for a week's study. Returning to Tejutla for ten days in mid-June, I concluded my studies in the Sierra Madre with several days at Serchil. The last few days of June and the first days of July were spent at Momostenango, and I brought my season to a close at Panajachel during the second week of the same month.

Though my field season of 1949 was devoted primarily to an investigation of the Pacific versant, I carried on some studies at stations which yielded data pertinent to this account. At the conclusion of my dry-season studies on the coastal plain and *boca costa,* I visited Granaja Lorena in the cloud forest during the third week in April. The second week of May, prior to the initiation of my wet-season studies on the coast, I spent at Granaja Los Ocales on the border between the southeastern and southwestern highlands. Upon completion of the wet-season studies on the coast, I devoted a month to tracing the border between the southwestern highlands and the Pacific versant proper. The last week of June I spent at Finca Santo Tomás, the second week of July at Yepocapa, and my studies of 1949 were concluded during the third week of July at Finca San Rafael at Dueñas. In addition to visiting these localities, I was fortunate enough to be able to spend some few hours on María Tucum in the course of various trips which necessitated my crossing the highlands.

In the following list of localities from which southwestern highland species have stemmed, I have given the dates during which collections were made at stations I visited. All elevations, given in meters, refer to the plazas in case of villages and to the *casa grande* in case of fincas. Distances are straight-line measurements.

ANTIGUA BASIN.—A large erosional (?) basin which has been cut into the escarpment facing the Pacific. It lies some 25 kilometers west and slightly south of Guatemala City and has an area of about 100 square kilometers. The rolling floor of the basin averages about 1500 m. elevation. It is well watered, and its climate suggests that it probably once supported a cover of savanna or mixed grassland and forest. To the south its entrance is flanked by the volcanoes Agua and Acatenango-Fuego; on the other sides the plateau slopes rise sharply from its floor to elevations of more than 2000 m. These, when uncultivated, support oak and oak-pine forests. During the Spanish colonial regime this area was the political, social, and cultural center of the *audiencia* of Guatemala, and it has been subjected to cultivation for more than 400 years. Today it is an important coffee center; the groves are heavily shaded, deeply mulched, and well cared for. Corn and pasture land occupy much of the basin floor. Within the basin lie such well-known collecting sites as Dueñas (Godman and Salvin), Antigua (Mission scientifique), and Pueblo Viejo (Slevin).

Argueta.—The "Arguetta" of the *Mission scientifique,* this little village lies in the pine-cypress zone between Sololá and Totonicapán. I have not crossed, nor do I ever intend to cross, the miserable trail that leads to the place. Altitude, about 2900 m.

Atitlán Basin.—A structural basin lying some 65 kilometers west of Guatemala City and occupied almost entirely by Lake Atitlán. The lake surface is at an elevation of 1550 m., and the plateau slopes rise from the water in almost sheer cliffs to elevations of 2000 m. on all but the south side. On the south the volcanoes San Pedro and Tolimán-Atitlán shield it from the Pacific. On the north side, where deep barrancas carry mountain torrents to the lake, small deltas have developed, and these constitute almost the only level terrain in the basin. The original vegetation of this basin and the escarpment slopes was probably a chapparal-like brush. On the deltas and less rugged terrain the coffee groves and the vegetable gardens of the Indians occupy most of the land, and milpas cling to the rugged slopes. Around the lake are many Indian villages, of which Panajachel (Tzanjuyú), San Lucas, and Santiago have served as bases for a host of biologists.

Chichavac.—The "Chichivac" of Slevin and Schmidt. It is an hacienda in the oak-pine zone about 5 kilometers north of Tecpán at about 2600 m. elevation (see Slevin, 1939: 395).

Chichicastenango.—An Indian village lying 10 kilometers south of Santa Cruz Quiché in the oak-pine zone; the surrounding terrain is of high relief. The land is cultivated with moderate intensity, and there are some fine stands of virgin oak and pine in the vicinity. Only occasional herpetological specimens have stemmed from this locality. Altitude, about 1950 m.

Chimaltenango.—An important commercial and political town about 35 kilometers due west of Guatemala City. It straddles the continental divide and is within the oak-pine zone. The surrounding country is of moderate relief and represents a major corn and wheat district. Little virgin forest remains in the region. Like Chichicastenango, it has never served as a base of any importance for herpetologists. Altitude, about 1800 m.

Dueñas.—A small village lying in the southwestern corner of the Antigua Basin. Coffee, corn, and pasture occupy most of the land in the region, and the surrounding escarpment slopes support a cover of scrubby oak. Formerly, a small lake lay just to the north of the village, and there is still much swamp land in its old basin. The locality was made famous by Godman and Salvin and their associates. My own base was at Finca San Rafael on the outskirts of the village. Altitude, about 1450 m. July 16-21, 1949.

El Potrero, Finca.—A Slevin locality at Pueblo Viejo (Slevin, 1939: 394) in the Antigua Basin, see Antigua Basin.

Godines.—A hamlet on the road between Panajachel and Patzum, the environs of which overlook Lake Atitlán from the northeast. The surrounding terrain is of moderate relief, and there are some fine stands of oak and pine in the vicinity. Wheat occupies most of the cultivated land in the region. This is a *Mission scientifique* minor locality. Altitude, about 2100 m.

GUATEMALA CITY.—The capital of Guatemala, at latitude 14° 38′ N. and longitude 90° 31′ W. It lies in the broad valley of Las Vacas, the floor of which is deeply dissected by barrancas. Originally parts of the area were covered with marshland and some still exists in the southern part of the city. Except on the valley slopes to the east and west, the original cover has long since disappeared. The plateau above the valley rises to some 2000 m., and areas of virgin-like cover are readily accessible from the city. Oak and pine undoubtedly represented the original vegetation of the region. It seems quite possible that specimens of Plateau species labeled "Guatemala" may have originated from the environs of the city. Altitude, 1485 m.

IXCHIGUÁN.—A hamlet on the rolling high surface of the Sierra Madre about 25 kilometers north and slightly west of San Marcos, the commercial and political center of the region. The village is dominated by Cerro Cotzic, which with an elevation of 3600 m. is probably the highest nonvolcanic peak in Central America. Though in the pine-cypress zone, the high plains are covered mostly with bunchgrass and the alpine meadows with short grasses and herbs. In the Ixchiguán area there are several fine stands of pine and pine-balsam. Most of the land is given over to the pasturing of sheep, and a few potatoes are cultivated in the vicinity of the village. Altitude, about 3200 m. April 22-25 and June 2-5, 1947.

LAS NUBES.— A structural block of considerable size lying between San José Pinula and Mataquescuintla east and slightly south of Guatemala City. It is sparsely inhabited and contains extensive stands of virgin oak and pine forests with a more mesic forest in the numerous barrancas that cut back into the block. The relief throughout the block as a whole is extremely high. I collected here only briefly in the western section, from Los Ocales as a base. Collections were made at elevations varying from 1900 m. to 2300 m.

LORENA, GRANAJA.—A small dairy farm in the cloud forest on the Pacific versant. Though several hours by bus from Quezaltenango, it is only 12 kilometers west of it. The entire area was covered with a deep layer of ash from the eruption of Volcán Santa María in 1902, and mountain freshets have since cut barrancas into the unconsolidated material. Here, and again at Yepocapa, I encountered a mixing of the Plateau and Pacific versant faunas. Altitude, about 1700 m. April 18-21, 1949.

LOS OCALES, GRANAJA.—A small farm on the ridge directly east of Guatemala City. The high rolling plains are intensively cultivated. The remaining virgin cover in the region suggests an original vegetation of oak and pine. From this base I was able to study the high block of Las Nubes. Only remnants of the southwestern highland fauna occur in this region. Altitude, about 2000 m. May 9-13, 1949.

María Tucum.—The local name applied to the high structural block lying between Los Encuentros (75 kilometers west of Guatemala City) and Totonicapán. The high level surface of this block is rolling and supports fine stands of pine and pine-cypress with openings of bunchgrass and short grasses. Aside from some lumbering, the area is utilized only for sheep-grazing. Since the main modern road and many of the older trails cross the area, many naturalists, like myself, collected occasional specimens from the area. I am of the opinion that the label "heights above Totonicapán," so frequently encountered on older specimens, refers to material which originated in this region. The crest averages some 3100 m. elevation. Cerro María Tucum and Cerro Quiché rise several hundered meters above the more or less level surface.

Momostenango.—An Indian village in the rugged barranca country, some 20 kilometers north of Totonicapán. The region is well watered, deeply dissected, and badly eroded. It supports a large Indian population, but is not particularly heavily cultivated. Although in the oak-pine zone, the cover of most of the region is pine parkland in which oak is not a conspicuous feature. Altitude, about 2300 m. June 27–July 1, 1947.

Panajachel.—A small village on the delta of the Rió Panajachel on the north side of Lake Atitlán, see Atitlán Basin. October 12–17, 1944; March 12-20 and July 7-12, 1947.

Patzicía.—Variously spelled Patzizía, Pazicilla. A village which lies on the rolling plains of the oak-pine zone about 40 kilometers west of Guatemala City and looks down to the Pacific through the headwater valleys of the Río Coyolate. The surrounding area is intensively cultivated by a sizeable Indian population. A *Mission scientifique* locality. Altitude, about 2100 m.

Quezaltenango.—The second city of Guatemala, lying some 110 kilometers west of Guatemala City. It is in a well-watered, erosional valley from which the slopes of the plateau crest rise abruptly. The valley is extensively grazed and produces food crops, while the slopes support a cover of pine. Protected from the Pacific by the volcanoes Santa María and Cerro Quemado, the valley in relatively dry and probably once supported a cover of short grass. The center of an enormous population of Indians in pre-Columbian times and since then an important commercial center, the original biota has probably suffered accordingly. Many naturalists have gathered occasional specimens from the environs. Altitude, 2335 m.

San Lucas.—A village at the base of Volcán Tolimán on the southern shore of Lake Atitlán. The surrounding country is, wherever possible, planted in coffee and milpa (maize), but most of the land is a rugged mass of black, basaltic lava, see Atitlán Basin. The ornithologist A. W. Anthony and the members of the *Mission scientifique* both collected material at this station, and I worked the area from Finca Santo Tomás along the road to Patulul.

San Rafael, Finca.—A finca on the outskirts of Dueñas, see Dueñas. Altitude, 1475 m.

Santa Cruz Quiché.—Capital of the department of El Quiché located in the oak-pine zone some 75 kilometers northwest of Guatemala City. The terrain and vegetation are similar to that of the Chichicastenango region. Robert Miller collected a few specimens here for the United States National Museum. Altitude, about 2000 m.

Santa Elena.—An hacienda in the pine-cypress zone above Tecpán. Both Slevin and Schmidt collected at this station as did C. M. Barber early in the century (see Slevin, 1939: 395).

Serchil.—A hamlet on the crest of the Sierra Madre, 10 kilometers north of San Marcos, the main center of the region. The terrain is similar to that encountered at Ixchiguán, but there is some difference in the vegetation. Although both lie within the pine-cypress zone, the forest is far more extensive in the Serchil region than it is at Ixchiguán. Altitude, about 3200 m. June 20-22, 1947.

Sololá.—The capital of the department of Sololá. The village lies in the oak-pine zone on the cliffs above Lake Atitlán and some 65 kilometers west of Guatemala City. Like Godines, not far distant to the east, the region is an important wheat district, but there are fine stands of both pine and oak in the environs. Members of *Mission scientifique* apparently stopped here briefly. Altitude, 2100 m.

Tacaná.—A village on the northwestern flank of the Sierra Madre 25 kilometers northwest of San Marcos. The surrounding country is of extremely high relief owing to the streams, headwaters of the Río Coatán (Chiapas, Mexico), which have deeply dissected the entire northern face of the sierra. In the oak-pine zone, the cover is largely a mixed forest and rather scanty, since the district is fairly extensively cultivated. Altitude, about 2500 m. April 8-13, 1947.

Tecpán (Tecpam).—A town 65 kilometers west and slightly north of Guatemala City, marking the eastern terminus of the main ridge which forms the backbone of the southwestern highlands. It lies in the oak-pine belt, and the terrain is much like that encountered at Chimaltenango. The region is intensively cultivated. Nearby Chichavac and Santa Elena above the town were collecting sites of Slevin (1939: 395) and Schmidt. Altitude, about 2300 m.

Tejutla.—A village on the eastern flank of the Sierra Madre about 20 kilometers north of San Marcos. The sierra slopes are here cut by the headwaters of the Río Cuilco and, as in the Tacaná region, the terrain is of extremely high relief. It is in the oak-pine zone, and the dominant cover type is oak, though occasional fine stands of pine are encountered in the region. Cultivation in the region is intensive, considering the rugged nature of the land. Altitude, about 2500 m. March 27-April 3, and June 9-17, 1947.

Totonicapán (Totonicapam).—A town in the oak-pine zone about 20 kilometers northeast of Quezaltenango. It lies in one of the tributary valleys of the Río Samalá, the main valley of which is entered from the south through Quezaltenango. The terrain is much like that in the region of Quezaltenango, except that there is less level land. The valley bottoms are intensively cultivated, and the slopes above the valleys support a magnificent cover of pine. Apparently, members of the *Mission scientifique* spent some time in the region, but only occasional reptilian and amphibian specimens have originated in the immediate vicinity of the town. Altitude, about 2500 m.

Volcán Agua.—The volcano dominating the Antigua Basin on the southeast, see Antigua Basin (Slevin, 1939: 394).

Yepocapa.—A village on the Pacific versant about 50 kilometers west and slightly south of Guatemala City. It lies in the cloud-forest zone, and like all of the Pacific face of the Plateau, the environs of the village are made extremely rugged by the many mountain torrents that have cut deep barrancas into the escarpment. As at Lorena, there were a few highland species that spill over on the Pacific versant. From here I was able to spend several days collecting on the north face of Volcán Acatenango, where typical Plateau species were encountered. Altitude, 1525 m. July 6-15, 1949.

APPENDIX II

LIST OF SPECIES

All species of amphibians and reptiles known to occur within the limits of the Chimaltenangan life area are listed. As stated in the Introduction, an attempt has been made to assemble all records of the species which have stemmed from the area. Material which has previously been reported is listed in the synonymies, but, only specimens which are recorded for the first time are designated by number. Most of these I have examined personally. Full citation in the synonymies is given only in the case of the original description; other records are listed more briefly, since they may be found in the Literature Cited. Literary references have not been included.

Even though secured slightly beyond the limits of the life area proper, all records of Chimaltenangan endemics, such as *Tropidodipsas fischeri* from Lorena, are included in the list. In some instances, where they have been secured along the fringes of the Chimaltenangan, several species belonging to other faunas have been included such as *Ameiva undulata parva* from the heights above Panajachel.

Unless otherwise noted all material listed by number is contained in the collections of the Museum of Zoology, University of Michigan. Abbreviations of other institutions whose material is included are: M.C.Z. (Museum of Comparative Zoology, Harvard College), C.N.H.M. (Chicago Natural History Museum), U.S.N.M. (United States National Museum).

All lengths are given in millimeters and elevations in meters.

Magnadigita morio (Cope)

Oedipus morio, Cope, *Proc. Acad. Nat. Sci. Phila.*, 1869: 103 (type locality, mountains of Guatemala); Cope, 1887: 8 (reference to type); Schmidt, 1936: 154 (Chichavac).
Geotrition morio, Smith, 1877: 74 (probable reference to type).
Spelerpes bocourti, Brocchi, *Batrachia, Mission scientifique au Mexique*, 1883: 111, Pl. 18, Fig. 2 (type locality, "hauteurs de Tonicapam [=Totonicapán], Guatemala").

Volcán Acatenango, between Yepocapa and Dueñas, Nos. 100489–90 (9).

Taylor's arrangement of *Bolitoglossa* (s.l.) is accepted herein, because it simplifies geographic discussion of an otherwise unwieldly genus.

The above specimens are assigned to this species only tentatively. From Chichavac material secured by Slevin, they differ in being much darker, which may or may not be the result of differences in preserving techniques. Furthermore, the light markings characteristic of the Chichavac material and commented upon by Schmidt (1936: 154) are either entirely lacking in my specimens or at best are only very obscure. The irregular alignment of the teeth on the vomerine, also characteristic of *morio*, is barely noticeable in the Acatenango specimens. Nevertheless, considering the paucity of *morio* material and the fact that my specimens were secured in a typical *morio* habitat (oak) not very far from the probable type locality of that species, a new name seems hardly warranted. This cannot be considered a record for the species on the volcanoes, since the north slopes of Acatenango from which the specimens were secured, are, at that point, contiguous with the Plateau.

Though Slevin secured the species in considerable numbers at Chichavac in July and August (Schmidt, 1936: 154-55), dry-season collecting by Schmidt in February produced but a single specimen in the same area. The specimens from Acatenango were taken in early July. It is entirely possible that my failure to secure the species in the oak zone in the Sierra Madre was owing to the early dates of my collecting in the region.

The specimens listed above were all secured from within or from beneath rotting oak logs in a very wet oak forest at approximately 2700 m. elevation. The females contained no ova in their body cavities.

Magnadigita rostrata (Brocchi)

Spelerpes rostratum, Brocchi, *Batrachia, Mission scientifique au Mexique*, 1883: 112 (type locality, "hauteurs de Tonicapam [=Totonicapán], Guatemala").

Oedipus rostratus, Dunn, 1926: 384 (Sierra Santa Elena, 9500 feet); Schmidt, 1936: 155 (Santa Elena and Cerro Quiché).

Ixchiguán, Nos. 98276, 98277 (3), 98278 (2); María Tucum, Nos. 98123 (4), 100491 (9), 100531 (3), U.S.N.M. 10032 (field number); Serchil, No. 98279.

For all practical purposes the material secured from the María Tucum block may be considered topotypic. The various localities at which the species has been collected in that region are all high and lie within the pine-cypress zone.

Though abundant in the María Tucum and Santa Elena (Schmidt, 1936: 155) areas, I found relatively few specimens in the Sierra Madre. Though occasionally secured from among the roots of bunchgrass, it is most common within rotting pine logs, especially when these are scattered along the edges of pine groves, rather than within the forest proper. The Serchil specimen was secured at the edge of a patch of a very wet grove of gigantic oaks. The species is undoubtedly restricted to the pine-cypress zone at elevations above 2900 m.

Schmidt reported (1936: 156) the discovery of an egg mass of this species in February, and the series in the United States National Museum, secured in mid-August, was accompanied by a mass of some 20 eggs. Female specimens secured by me in early August contained eggs in the body cavity ready for deposition. A fairly extensive breeding season is indicated.

Pseudoeurycea rex (Dunn)

Oedipus rex, Dunn, *Proc. Biol. Soc. Wash.*, 34 (1921): 143 (type locality, Sierra Santa Elena near Tecpán, Guatemala, altitude 9500 feet); Dunn, 1926: 366 (reference to types); Schmidt, 1936: 165 (Santa Elena including types; Cerro Quiché).

Ixchiguán, Nos. 98280 (28), 98281 (20); María Tucum, No. 100530; Serchil, No. 98282 (4); Tecpán, M.C.Z. Nos. 12096–12100 (*fide* Arthur Loveridge).

Material at hand indicates that this species is badly in need of revision. I have pointed out (1943*a*:19) that specimens from the Cuchumatán Mountains assigned to this species are slightly atypical, and the Sierra Madre material is certainly puzzling. The Ixchiguán material seems typical, but the Serchil specimens closely approach *goebeli* in possessing very long limbs, though they lack the characteristic light marbling on the undersurface of the tail of that species. Since the Sierra Madre in the Serchil region is contiguous with the northern slopes of Volcán Tajumulco, the type locality of *goebeli,* the species might be expected at Serchil. The specimens are, however, morphologically closer to *rex* than to *goebeli,* so that until further material is forthcoming from other highland localities in Guatemala, the details of variation in the two species must remained unsolved, and the Serchil specimens are here considered *rex.*

At Ixchiguán the species was relatively abundant and was most generally found at the base of bunchgrass clumps or beneath logs on the open plains. I did not secure it in the forests of that region, whereas at Serchil it occurred only in the pine-cypress forest. The Tecpán specimens undoubtedly stemmed from the mountains above the town.

Females secured during the first week of June contained ova in various stages of development within the body cavities.

Bufo bocourti Brocchi

Bufo bocourti, Brocchi, *Bull. Soc. Philomath.,* 1877: 186 (type locality, Totonicapán).

Chichavac, C.N.H.M. Nos. 20252–3; Ixchiguán, No. 98253 (27); Lorena, No. 100505(10); María Tucum, Nos. 100517, 100529; Momostenango, Nos. 98254(13); Panajachel, No. 98258; Panajachel (heights above), No. 98334 (juveniles and tadpoles); Patzicía, No. 100527 (tadpoles); Santa Elena, Nos. 85109, C.N.H.M. 1791, 1792 (4), 20227, 20233, 20236–7, 20751–2; Tacaná, Nos. 98251(19), 98256, 98335 (tadpoles); Tecpán, M.C.Z. No. 12845 (*fide* Arthur Loveridge); Tejutla, Nos. 98252(26), 98256, 98257; Totonicapán, U.S.N.M. No. 123684.

This species is the most abundant and most widely distributed of the Plateau amphibians. As an adult it is largely terrestrial, which may account for its ability to transcend terrestrial barriers which more aquatic amphibians might find insurmountable. It breeds normally in ponds and springs, but can cope with quiet water in streams when necessity demands. Its breeding season is apparently year-round. I have found its egg masses at Tacaná in mid-April, clasping pairs at Ixchiguán in early June, and gravid females at Momostenango late in the same month. Young tadpoles were secured near Patzicía in early July and newly transformed juveniles as early as mid-March above Panajachel and as late as early August on María Tucum.

Aside from a specimen secured in Lake Atitlán at the mouth of the Río Panajachel following a flash flood and undoubtedly washed down from higher elevations, the lowest record of its occurrence is 1700 m. at Lorena.

Plectrohyla cotzicensis Stuart

Plectrohyta cotzicensis (=Plectrohyla cotzicensis) Stuart, *Proc. Biol. Soc. Wash.,* 61 (1948): 17 (type locality, 2 km. northwest of Ixchuguán, San Marcos, Guatemala). Elevation, about 3500 m.).

Ixchiguán, Nos. 95902 (holotype), 95903–7 (paratypes), 98339–40 (tadpoles); María Tucum, Nos. 100508, 100518–19 (tadpoles).

The discovery of a single female specimen and tadpoles at several localities on María Tucum at approximately 3100 m. confirms my earlier suggestion (1948*a*:18) that this species, like *Pseudoeurycea rex* and *Magnadigita rostrata* is discontinuously distributed along the crest of the higher ranges surmounting the Plateau and is endemic to the pine-cypress zone. The following is the description of the tadpole anticipated in the type description.

Body pear-shaped, slightly broader than deep. Eyes and nostrils almost dorsad, the former about one-third the way back on the body. Anus slightly dextral. Spiracle sinistral and lateral, slightly over one-half the way back on the body. Tail varying from 1.4 to 1.6 times the body length; three to four times as long as deep; fins not extended on the body and only very slightly longer than the tail musculature.

Mouth almost terminal, directed downwards, equal in width to the interorbital distance (Pl. VII, Fig. 3). Lips fringed with a single row of small papillae except in almost metamorphosed specimens, in which a double row of fringing papillae may appear laterally or on the lower lip. A row of papillae of larger size between both the upper and lower lips and the teeth, the former generally only weakly developed. No lateral patch of papillae. Tooth rows, 2/3. When fully developed, the anterior rows subequal in length and extending almost to the corners of the mouth; inner anterior row of teeth broken medially. Posterior tooth rows shorter than anterior ones; the inner and median rows slightly longer than the beak. The outer row, when fully developed, equal to the beak length. Beak about one-third as long as the mouth width; only slightly arched and set with sharp denticulations. Body dark brown above; tail brownish gray; both fin and musculature mottled with dark brown.

Specimens smaller than 10 mm. in body length do not have fully developed mouth parts. Leg buds are developed when the tadpole reaches about 17 mm. body length. Maximum size, about 20 mm. body length, may be reached before the leg buds show any development. From that stage until the forelegs break through, there is a gradual decrease in body length, and when transformation takes place the body length is only slightly more than 16 mm.

The species apparently has an extended breeding season, a condition which seems to obtain in most of the stream salientians of Guatemala. Females with eggs apparently ready for deposition were secured at Ixchiguán on April 23, and one in the same condition was taken on María Tucum on August 4. Tadpoles as small as 6 mm. and at the transformation stage were secured during early and mid-April at Ixchiguán, while transformed juveniles were taken on María Tucum on August 4.

Both tadpoles and adults have been taken in the tiny rivulets in the pine-cypress zone and in quiet spring-fed pools, in which the species is associated with *Bufo bocourti*. Thus, though apparently adapted to life in the swift mountain streams, the species can and does invade the lenitic environment.

Plectrohyla guatemalensis Brocchi

Plectrohyla guatemalensis, Brocchi, *Bull. Soc. Philomath.,* 1877: 92 (type locality, Pacicilla [Patzicía], Guatemala); Hartweg, 1941: 5 (Panajachel, Guatemala).
Cauphias guatemalensis, Brocchi, 1877: 129 (type of *Plectrohyla guatemalensis);* Barbour, 1927; 96 (Panajachel, Guatemala); Kellogg, 1932 119 (Panajachel, Guatemala and reference to type).

Las Nubes, Nos. 100520 (tadpoles), 100523 (tadpoles); Momostenango, Nos. 95909–10; Panajachel, Nos. 95913–4, 98338 (tadpoles); Tacaná, 95911, 98338 (tadpoles); Tejutla, No. 95912; Totonicapán, U.S.N.M. No. 123685 (tadpoles).

This is the only *Plectrohyla* known to occur in the oak-pine zone, and it is one of the species which indicates faunal relationship between the Las Nubes block to the east of Guatemala City and the southwestern highlands. Though occurring in the subhumid basin of Panajachel at 1500 m., the species is replaced on humid slopes at similar elevations by what I believe to be an undescribed species and/or *Plectrohyla sagorum.*

The tadpoles of this species are almost indistinguishable from tadpole form "x" of Stuart (1942*a*: 8–9, Figs. 1 and 2). The two, as well as the undescribed form mentioned above, have tadpoles quite unlike those of other members of the genus. In the *guatemalensis* type there is a double row of papillae bordering the lips, and the lower tooth rows are subequal in length. What may be referred to as the *sagorum* type, has only a single row of papillae bordering the lips (except occasionally individuals at the metamorphosing stage), and the lower tooth rows decrease in length from inner to outer. A more detailed discussion of the tadpole types will be presented in a forthcoming paper.

Rana macroglossa Brocchi

Rana macroglossa, Brocchi, *Bull. Soc. Philomath.,* 1877: 177 (type locality, Plateau of Guatemala); Brocchi, 1881; 12, Pl. 3, Fig. 1 (reference to type).
Rana maculata, Brocchi, *Bull. Soc. Philomath.,* 1877: 178 (type locality, Totonicapán, Mexico [in error]); Brocchi, 1881: 13, Pl. 3, Fig. 2 (reference to type).
Rana halecina, Boulenger, 1920: 433 (types of *macroglossa* and *maculata*).

Chichicastenango, U.S.N.M. No. 123678 (tadpoles); Chimaltenango, U.S.N.M. Nos. 123635–7, 123638 (tadpoles), 125402 (tadpoles); Momostenango, Nos. 98236, U.S.N.M. 125317 (tadpoles); Río Molino (between Godines and Patzicía), Nos. 100528 (tadpoles), U.S.N.M. 125403 (tadpoles); Panajachel, Nos. 98232 (4), 98233 (5), 98234, 98235; Santa Cruz Quiché, U.S.N.M.

No. 125318 (tadpoles); Tejutla, No. 98330 (tadpoles); Totonicapán, U.S.N.M. No. 123685 (tadpoles); Yepocapa (uncatalogued material).

The status of this species is yet to be settled. There is on the highlands of northern Central America a frog of moderate size, which in most of its morphological characters is very close to the lowland *Rana palmipes.* Just what the relationship between the two is, I have been unable to determine, owing to a lack of *palmipes* material. The name *macroglossa* is used tentatively.

Regardless of the genetic relationships of the species, there can be no question as to its distinctness on the basis of tadpoles alone. I recorded (1948*b*: 40–41) and described the tadpole of an unknown hylid which I had secured in the mountain streams of Alta Verapaz. These may now be allocated to *Rana macroglossa.* It is by far the most frequently encountered tadpole in the upland streams of Guatemala. With the exception of certain ontogenetic changes (Table V), the material collected by me as well as the tremendous series secured by Robert Miller reveals that my previous description of the tadpole was correct in all essential details (Pl. VII, Figs. 1 and 2).

TABLE V

Ontogenetic Changes Noted in the Tooth-row Formula in a Series of Tadpoles of *Rana macroglossa*

Total Length (mm.)	Tooth Formula	Remarks
11.25	2/3	
12.25	3/3	
13.75	3/4	
14.75	4/4	Inner anterior row barely indicated
21.50	4/4	Inner anterior row well developed
27.50–59.00	5/4	Leg buds first evident in specimen with body length of 24 mm.; tail length unknown
62.00	6/4	Well-developed hind legs; forelegs visible through body wall

This species is the common frog of the lotic environment of the highlands and highland slopes of Guatemala to an elevation of about 2700 m. An extended breeding season is indicated for this species, since its tadpoles in various stages of development may be found the year round in mountain streams.

Rana pipiens Schreber

Rana pipiens, Schreber, *Der Naturf.* (Halle), 18 (1782): 185, Pl. 4 (type locality, North America, probably New York, *fide* Kauffeldt, 1936: 11).

Santa Cruz Quiché, U.S.N.M. No. 125319 (tadpoles); Tacaná, Nos. 98230(3), 98231(5), 98331 (tadpoles).

I have been unable to distinguish between the tadpoles of this species in Guatemala and those from various populations in the United States.

In contrast to *Rana macroglossa,* this species is limited to the lenitic environment. On the flood plain of the Río Panajachel, which is a braided stream along its lower course, the differences in the habitat of the two ranas is well brought out. Wherever isolated ponds occur on the flood plain only *Rana pipiens* was encountered, while in the main stream and its various channels only *Rana macroglossa* occurred. Even though the two habitats are but a few feet apart this strict selection of habitat is unvarying.

Though no less widely distributed over the southwestern highlands than is *macroglossa,* the infrequence of standing water in that rugged area results in a relative sparse population of *pipiens.* I have never secured the species above the oak-pine zone.

Hypopachus barberi Schmidt

Hypopachus barberi Schmidt, *Field Mus. Nat. Hist., Zool. Ser.,* 24 (1), (1939): 1–2, Fig. 1 (type locality, Tecpán, Sololá [now Chimaltenango], Guatemala).

Panajachel, Nos. 98240(3), 98241(4), 98242(2), 98336 (tadpoles).

The above series, all males, were collected in a marshy pond on the flood plain of the Río Panajachel, part in mid-March and the rest in early July. Males were singing at both times, but no females were seen. A series of tadpoles taken from a beach pool on the shores of Lake Atitlán on July 12 proved to be almost identical with those of *Hypopachus simus,* which I had previously described (1941: 127) and figured (1943*b*: Figs. 3–5). From *simus* tadpoles they differ in having a more rounded snout and a more slender tail. Like *simus* the inner part of the labial apron is bordered with fleshy tubercles, which suggests that tadpoles of the *inguinalis* group may differ from those of the *cuneus* group in this character.

In late June I heard hypopachi, presumed to be this species, singing at Momostenango. Scattered records of this species indicate that it is restricted to the oak-pine zone of the southwestern highlands except when it invades subhumid areas of slightly lower elevations in adjacent regions, for example, the Atitlán Basin. Its geographic pattern is, therefore, not unlike that of *Plectrohyla guatemalensis.*

Anolis crassulus crassulus Cope

Anolis crassulus, Cope, *Proc. Acad. Nat. Sci. Phila.,* 1864: 173 (type locality, Central Guatemala); Duméril and Bocourt *in* Duméril, Bocourt, and Mocquard, 1873: 82, Pl. 16, Fig. 17 (Plateau of Guatemala); Boulenger, 1885: 81, in part (Plateau of Guatemala).

Anolis crassulus crassulus, Stuart, 1942*b*: 1–2 (reference to types).

Anolis uniformis, Barbour, 1934: 153 (reference to cotype and Museum of Comparative Zoology material listed below); Slevin, 1942: 455 (Chichavac, San Antonio, Volcán Agua).

Atitlán, C.N.H.M. No. 2051; Chichavac, C.N.H.M. Nos. 20256(61), 20277(12), 20280(45); Ixchiguán, No. 98175; Las Nubes, No. 100501; Lorena, No. 100499; Los Ocales, No. 100500(6); Panajachel, Nos. 98180–2; M.C.Z. 24401–3 (*fide* Arthur Loveridge); San Lucas, M.C.Z. Nos. 24400, 27618–21 (*fide* Arthur Loveridge); Tacaná, Nos. 98165(11), 98166(10), 98173, 98174; Tecpán, Nos. 64327–9(16), M.C.Z. 24404–10 (*fide* Arthur Loveridge); Tejutla, Nos. 98167(3), 98168, 98169(2), 98170(2), 98171 (2) 98172 (2), 98176–7, 98178(4), 98179(2); Volcán Acatenango between Yepocapa and Dueñas, No. 100503; Volcán Agua, C.N.H.M. No. 20404; Yepocapa, Nos. 100502, 100504.

At no place on the highlands of Guatemala have I seen this species in the numbers in which it was secured by Slevin in the Tecpán area (Slevin, 1942: 455–56). The species is a climbing rather than a ground form and shows little habitat preference wherever it occurs, though it does appear to avoid stands of pure pine.

I did not encounter the species much above 2600 m., and it occurred only sparingly at 1500 m. at Panajachel. The single Ixchiguán specimen cannot be accepted as proof that the species invades the pine-cypress zone, since it was taken among some pine planks that had been brought in from lower elevations for the purpose of constructing a fence. Like both *Bufo bocourti* and *Plectrohyla guatemalensis* this species brings out the nature of the geographic pattern that obtains in most of the oak-pine reptiles. Wherever subhumid or only moderately humid conditions prevail at lower elevations (Panajachel and the Antigua Basin), these species descend to much lower elevations than they do along the humid slopes. At Lorena *Anolis crassulus crassulus* was not taken below 1900 m.

The occurrence of the species with *Plectrohyla guatemalensis* on the Las Nubes block to the east of Guatemala City indicates faunal relationship at higher elevations in that area to the southwestern highlands.

Anolis laeviventris (Wiegmann)

Dactyloa (Anolis) laeviventris, Wiegmann, *Herpt. Mex.,* 1834: 47 (type locality, Mexico).

Tectitán (10 km. north of Tacaná), No. 98910.

A single specimen provisionally referred to this species was collected in the pine zone on the northern flanks of the Sierra Madre above the arid Cuilco Valley at 1800 m. The species is not considered typical of the Plateau assemblage, but represents an exotic which enters the southwestern highlands only along its fringes.

Sceloporus malachiticus smaragdinus Bocourt

Sceloporus smaragdinus, Bocourt, *Ann. Sci. Nat., Zool. Ser.,* 5, 17 (1873): 1 (type localities, Sololá, Totonicapán, Quetzaltenango, Republic of Guatemala); Günther, 1890: 68 (Dueñas).

Sceloporus formosus, Boulenger, 1897: 501 (Dueñas).

Sceloporus formosus smaragdinus, Smith, 1939: 41 (San Lucas Volcano, Tecpam [Tecpán], Volcán Agua, Santa Elena, Atitlán, Sierra Santa Elena, Volcán Tajumulco, Chichavac, San Antonio); Slevin, 1942: 457 (Volcán Agua, Tecpam [Tecpán], Santa Elena, San Antonio.)

Sceloporus malachiticus smaragdinus, Smith, 1942*a*: 356 (name change, no specimens listed).

Dueñas, Nos. 100495(6), 100496(3), 100497(2); Ixchiguán, Nos. 98149 (15), 98150(24), 98151(19); María Tucum, Nos. 100498(2), U.S.N.M. 10016 (field number); Momostenango, No. 98159; Los Ocales, Nos. 100492–3; Panajachel, Nos. 98126(4), 98127, 98128(4), 98129(2), 98130 (1), 98132 (4), 98133 (2), 98134 (2), 98135 (8), 98136 (2), 98141 (3); San Lucas, No. 100494(9); Serchil, No. 98158(6); Tacaná, Nos. 98145(4), 98146 (5), 98147, 98148 (3); Tejutla, Nos. 98137 (4), 98138, 98139 (2), 98140, 98142 (2), 98143 (4), 98144 (3), 98152, 98153 (2), 98154 (21), 98155 (2), 98156–7.

This is by far the commonest reptile of the southwestern highlands. The species offers an excellent example of a phenomenon frequently observed in the region; namely, that much of the herpetofauna is distributed with reference less to the major environments than to some microfeature of those environments. Thus, this species has a high degree of tolerance for such major habitats as the oak-pine forests, grasslands, or chaparral and seems to avoid only the depths of the pine-cypress forest. Since it is a saxicolous form, its requirements appear to be primarily the presence of rock fields, rock walls, or even an abundance of old logs upon which it may climb. In open forests it may often be found clinging to the trunks of trees.

An example of its restriction to habitats providing conditions for climbing was noted at Ixchiguán. In one area which was studied intensively, an old stone wall ran through a dense cover of bunchgrass. In the bunchgrass proper the density index of the species (individuals observed/man-hours of observation) was zero (0), whereas along the wall on the same plains the index was 45. On a similar wall on short-grass plains in the same region, the index was 92, as opposed to zero (0) on the short-grass plains surrounding the wall. Possibly owing to the abundance of suitable habitats and the lack of other reptilian competition, the species attains its maximum abundance at high elevations for it was especially common on the Cotzic Pass above 3600 m. No other reptile attains such high elevations in Guatemala.

Wettstein (1934: 25) has noted that in Costa Rica individuals of *Sceloporus m. malachiticus* at high elevations attain a maximum size considerably less than those at lower altitudes, and Smith (1939: 45) believed the same to be true of *Sceloporus m. smaragdinus.* These two authors also noted a decrease in sexual dichromatism in populations from higher altitudes, but in comparing the population at Panajachel with that from Ixchiguán this could not be substantiated, although a definite maximum-size difference was noted. At the two localities an effort was made to secure as large adults as possible. At Panajachel (1500 m.) males larger than 80 mm. head-body length were not uncommon, the largest in my collection measuring 87 mm. At Ixchiguán (3200 m.) the largest male captured measured only 69 mm., though specimens longer than 60 mm. were not uncommon. Among the females the largest taken at Panajachel was 77 mm. long and at Ixchiguán the largest of the same sex did not exceed 65 mm. Females taken in early April showed no signs of ovogenesis, but those secured in early July contained mature eggs.

In descending to 1500 m. in the drier basins of Atitlán and Antigua and in avoiding the humid slopes at the same elevation, the species parallels *Anolis crassulus crassulus*. Though secured on the ridges immediately east of Guatemala City, this species was represented by the typical form on the Las Nubes block.

Sceloporus variabilis olloporus Smith

Sceloporus variabilis olloporus Smith, *Occ. Papers Mus. Zool. Univ. Mich.* 358 (1937): 11 (type locality, San Juanillo, Costa Rica).

Momostenango, Nos. 98160(2), 98161(2); Tectitán (10 km. north of Tacaná), No. 98164.

Like *Anolis laeviventris* this species cannot be considered a member of the fauna of the southwestern highlands proper. Wherever river valleys extend back into the Plateau from the north and northeast small populations of this species live on the very fringes of the Chimaltenangan area. This form occurred sparingly in open pine forests in the Momostenango region up to about 2300 m. and on the northern flanks of the Sierra Madre in the pine zone up to at least 1800 m.

Ameiva undulata parva Barbour and Noble

Ameiva undulata parva Barbour and Noble, *Bull. Mus. Comp. Zool. Harvard Univ.*, 59 (6), (1915): 476 (Guatemala).

Heights above Panajachel, No. 98205(2).

Like *Sceloporus v. olloporus* this species is not typically a member of the southwestern highlands fauna but merely enters its fringes along the south. Though extremely common in the vicinity of Panajachel at 1550 m., it occurred only sporadically along the margins of pine forests 500 m. above that village, and its vertical limit appears to lie in the neighborhood of 2000 m. in this only moderately humid region. On very wet slopes (Yepocapa) the species reached its vertical limit some 400 m. lower. Just as highland forms reach their lower limits in the drier parts of the Pacific versant, so do lowlanders appear to attain their upper limits under the same environmental conditions.

Barisia moreleti fulva (Bocourt)

Gerrhonotus fulvus, Bocourt, *Nouv. arch. mus. hist. nat. bull.,* 7 (1872): 104 (type locality, pine forests of Totonicapán on the west slopes of the Cordillera, 2460 m.), not seen; Bocourt, *in* Duméril, Bocourt, and Mocquard, 1878: 352, Pl. 21 B, Fig. 6 (reference to type).

Gerrhonotus moreleti, Günther, 1885: 41, Pl. 24, Fig. C (Dueñas); Boulenger, 1885: 278 (Dueñas); Slevin, 1942: 459 (Chichavac, Santa Elena).

Barisia moreleti fulva, Tihen, 1949*a*: 223 (. . . western Guatemala . . .); Tihen, 1949*b*: 598 (mention of race).

Chichavac, C.N.H.M. Nos. 20242–51, 20254(7), 20278(37); Chichicastenango, C.N.H.M. No. 20490; La Lorena, Nos. 100484, 100486, 100487(5); Santa Elena, C.N.H.M. Nos. 20226, 20287–8; Tecpán, C.N.H.M. No. 2511 (25); Volcán Acatenango between Yepocapa and Dueñas, No. 100488; Volcán Agua, C.N.H.M. No. 20405.

This form is apparently the most tolerant of the Chimaltenangan reptilian species as indicated not only by its vertical range but by its local distribution within its outer limits. Its presence in the very wet cloud forest at La Lorena is particularly surprising.

Though most commonly encountered in forest debris (Slevin, 1942: 439) and among the roots at the base of clumps of bunchgrass, the individuals are occasionally seen sunning on logs or on the ground in sunny openings in the forest. Slevin secured juveniles of the species in July and August (1942: 439; 1939: 395) in the Tecpán region, and I secured fairly well-grown juveniles at Lorena in mid-April. These retained a trace of the umbilical scar. In the Sierra Madre this form is replaced by *Barisia moreleti rafaeli.*

Barisia moreleti rafaeli (Hartweg and Tihen)

Gerrhonotus moreleti rafaeli, Hartweg and Tihen, *Occ. Papers Mus. Zool., Univ. Mich.,* 497 (1946): 8 (type locality, 16 km. south of Siltepec, Chiapas, at 2300 m. elevation).

Barisia moreleti rafaeli, Tihen, 1949*a*: 223 (southern Sierra de Chiapas and Volcán Tajumulco); Tihen, 1949*b*: 598 (mention of race).

Ixchiguán, Nos. 98217–20, 98221(2), 98223, 98224(2), 98225–6; Tacaná, shed skin (uncatalogued); Tejutla, No. 98222 (4); Serchil, No. 98227 (2).

As is well known to those who have had to discriminate between races of this species, the identification of individuals is difficult. In dealing with several populations and occasional individuals from various localities on the southwestern highlands some very atypical individuals have been encountered. Within the range of *fulva,* the single individual known from Chichicastenango is almost a typical *temporalis,* whereas the single specimen from above Yepocapa is a good *salvadorensis.* In the population from the Sierra Madre variability is such that intergradation is indicated with a tendency toward *rafaeli* rather than *fulva.* An analysis of the frequency of the several diagnostic characters of *rafaeli* and *fulva* and of the same characters in the Sierra Madre population is given in Table VI.

TABLE VI

Comparison of Several Characters in Various Populations of *Barisia moreleti*

Figures in parenthesis indicate number of specimens; figures in columns are percentages. Data for *Barisia m. rafaeli* from Hartweg and Tihen (1946: Table IV). Data for *B. m. fulva* based upon a series of specimens (38) from the Tecpán region. The total for Sierra Madre is a summation of the Ixchiguán, Tejutla, and Serchil series.

Character	Ixchiguán (11)	Tejutla (4)	Serchil (2)	Sierra Madre (17)	*fulva*	*rafaeli*
Postnasals separated	64	0	100	56	13	100
Posterior prefrontals present	81	100	25	80	1	100
Posterior loreal in contact with supralabials	86	100	100	90	12	100

Like *Baraisia moreleti fulva,* this race has an extensive altitudinal range and within that area displays a high degree of tolerance to microenvironments. Newly born juveniles were taken at Ixchiguán in early June.

Abronia vasconcelosii (Bocourt)

Gerrhonotus (Abronia) vasconcelosii, Bocourt, *Nouv. arch. mus. hist. nat. bull.,* (1872): 107 (type locality, "Arguetta" [=Argueta], western Guatemala), not seen.
Abronia vasconcelosii, Tihen, 1949*b*: 591 (allocation to genus).

This species is known only from the unique type. H. M. Smith (1942*a*: 346) and Tihen (1949*b*: 590) are both of the opinion that the species is very probably arboreal, which may account for its having been overlooked by collectors. On the basis of the single known specimen, the species must be considered an inhabitant of the pine-cypress zone.

Thamnophis eques fulvus (Bocourt)

Eutaenia cyrtopsis fulvus, Bocourt, *Mission scientifique au Mexique,* (1893): 777, Pl. 62, Fig. 2 (type locality, Alta Verapaz).
Thamnophis scalaris, Ruthven, 1908: 129 (Tecpán).
Thamnophis eques, Slevin, 1939: 397 (Chichavac, Lake San Antonio, El Potrero).
Thamnophis sumichrasti fulvus, Smith, 1942*b*: 112 (Sierra Santa Elena, Chichavac).

Ixchiguán, Nos. 98293–4; Las Nubes, Nos. 100513–4; Tacaná, Nos. 98288–92; Tejutla, Nos. 98295–97.

This species is the commonest and most wide-ranging of the ophidians of the southwestern highlands. It seems to avoid only very dense forests and is most frequently met with in the vicinity of water. In the oak-pine zone it was often associated with piles of brush and was occasionally encountered on grassy slopes in open pine forests. On the high bunchgrass plains of the pine-cypress zone it was secured generally along streams. Specimens from Ixchiguán contained tadpoles in their stomachs, and one specimen contained an adult of *Plectrohyla cotzicensis.*

In the vicinity of Tecpán, Slevin (1939: 397) found it only in the oak-pine zone, but in the Sierra Madre I found the species at 3300 m. and it may be assumed that it goes even higher.

Data presented by Slevin (1939: 397) and by myself (1943*b*: 22 and 1948*b*: 63) indicates that the Plateau population of this form has a slightly higher average number of abdominals than populations from the Cuchumatán Mountains and Alta Verapaz. This difference, however, does not appear distinct enough to warrant subspecific separation.

The only unvarying scale character of taxonomic significance in the series available is the oculars, which are uniformly 1–3. Variable morphological characters are presented in Table VII.

TABLE VII

Variations in Major Morphological Characters in *Thamnophis e. fulvus*

Lengths refer to total head-body-tail length, with the figure for that of the tail in parentheses.

Number	Sex	Dorsals	Abdominals	Subcaudals	Labials	Temporals	Lengths
98288	♂	19–17–15	149	71	8/10	1+4/1+2	590 (120)
98290	♂	19–17–15	149	68	8/10	1+2/1+4	510 (120)
98294	♂	19–17	151	71	6/?	1+1	490 (120)
98295	♂	19–17	144	..	8/9–10	1+2/1+4	....
98296	♂	19–17	145	..	8/10–11	1+2	....
100513	♂	19–17	147	70	8–7/10	1+3	375 (90)
98289	♀	19–17	143	62	9–8/10–11	1+3/1+2	660 (150)
98291	♀	19–17–15	152	59	8–9/10	1+2/1+1	195 (40)
98292	♀	19–17	143	61	9–8/10	1+2	465 (100)
98293	♀	19–17	146	59	*	*	*
98297	♀	19–17	151	..	8/10	1+2	685 (175)
100514	♀	19–17	145	62	8/10	1+2/1+3	660 (135)

*Head Damaged.

Pituophis deppei lineaticollis (Cope)

Arizona lineaticollis, Cope, *Proc. Acad. Nat. Sci. Phila.,* 1861: 300 (type locality, Mexico).
Pituophis lineaticollis, Slevin, 1939: 400 (Volcán Agua).

Chichavac, C.N.H.M. No. 1927 (not seen).

This is another species which enters the Chimaltenangan life area only along border regions. Records indicate that, like the following species, it is a form restricted primarily to intermediate elevations.

Rhadinaea lachrymans (Cope)

Lygophis lachrymans, Cope, *Proc. Amer. Phil. Soc.,* 11 (1869): 154 (type locality, unknown).
Liophis lachrymans, Slevin, 1939: 401 (Chichavac).

I did not secure this species any place on the southwestern highlands, though it was not uncommon on the humid Pacific versant at 1450 m. Bailey (1940:6) recorded it from 1650 m. on the Pacific slope of Chiapas. The species is not a typical member of the herpetofauna of the Chimaltenangan, but may invade the fringes of the region, according to Slevin's record (1939: 401) of the species in the oak-pine zone at Tecpán.

Rhadinaea godmani (Günther)

Dromicus godmanni, Günther, *Ann. Mag. Nat. Hist.,* 15 (1865): 94 (type locality, Dueñas, Guatemala).
Liophis godmani, Slevin, 1939: 401 (Chichavac).

Chichavac, C.N.H.M. No. 20263; Dueñas, No. 100516; Tejutla, Nos. 96647–50.

All specimens from Tejutla were secured from beneath piles of oak and pine trimmings in the oak-pine zone between 2350 and 2600 m. Slevin (1939: 401) found the species at similar elevations in the Tecpán region. On the trail between Tejutla and Ixchiguán I found the mutilated tail of a specimen at about 3000 m. I do not believe that the species invades the pine-cypress zone, however, and I suspect that the tail found at the higher elevation possibly had been carried up from lower altitudes on the hoof of a mule, which had probably unknowingly killed the animal at some lower point.

The series from Tejutla are slightly atypical in several respects. In only a single specimen (No. 96645) does the typical labial count (8/9) occur. In pattern, the dark stripe extending from the eyes across the penultimate supralabial, a characteristic feature of *godmani,* is lacking, and the primary body stripes on the sides are narrower. In the typical form these stripes are disposed on scale rows 4 (1/2)–5–6 (1/2), but in the Tejutla population they are only on scale rows 4 (1/2)–5. In the Tejutla specimens the secondary stripes are more definitely defined, especially in the juveniles, than in topotypic and near topotypic material. Despite these variations Dr. Joseph

TABLE VIII

Variations in Major Morphological Characters in *Rhadinaea godmani*

Lengths refer to total head-body-tail length, with the figure for that of the tail in parentheses.

Number	Sex	Abdominals	Subcaudals	Labials	Lengths
96647	♂	174	93	7/8	355 (110)
96648	♂	176	89	7/8	420 (135)
96649	♂	175	90	8/9	190 (55)
100516	♂	171	88	8/9	390 (110)
96650	♀	175	75	7–8/8–9	170 (40)

TABLE IX

Variations in Major Morphological Characters in *Geophis rhodogaster*

Number	Sex	Abdominals	Subcaudals	Labials	Lengths
98309	♂	131	43	6/6	290 (65)
100515	♂	131	40	6/?	....
98310	♀	138	32	5/6	215 (35)
98308	♀	138	33	6/6	170 (25)

Bailey, who is fully familiar with the genus, informed me that in his opinion this slightly aberrant population does not warrant taxonomic recognition.

In the discussion of the *godmani (lachrymans)* group of *Rhadinaea* by Stuart and Bailey, (1941) the diagramatic representation of the *godmani* pattern in Figure 1 is incorrect. For this error I must assume complete responsibility, since Dr. Bailey was absent from this country and did not have an opportunity to check the diagram.

All the specimens listed above have the dorsals disposed in 21 rows throughout the body length, the oculars are 1–2 and the temporals 1+2. Variable morphological characters of the material is given in Table VIII.

Geophis rhodogaster (Cope)

Colophrys rhodogaster, Cope, *Proc. Acad. Nat. Sci. Phila.,* 1868: 132, Fig. (type locality, neighborhood of the city of Guatemala).

Catostoma rhodogaster, Slevin, 1939: 407 (Chichavac).

Las Nubes, No. 100515; Tacaná, Nos. 98308–09; Tejutla, No. 98310.

Except for the Las Nubes specimen which was found crushed on a road in the oak zone at 2050 m., the rest of the material was secured in the oak-pine zone at 2400 m. These were taken in the Sierra Madre from beneath logs and brush piles and were associated with *Barisia m. rafaeli* and *Rhadinaea godmani,* and in one instance with *Thamnophis e. fulvus.* Slevin (1939: 407) secured this species at 2600 m. in the Tecpán region. The occurrence of the species on the Las Nubes block indicates that the Plateau assemblage persists in dilute form, at least, at higher elevations east of Guatemala City.

In all the specimens, except the mutilated one (No. 100515), the dorsals are smooth and disposed in 17 rows throughout the body length; there is no praeocular, 1 postocular, and a single temporal. The fifth supralabial is in contact with the parietal and the first pair of sublabials are broadly in contact. Variable morphological features are listed in Table IX.

Tropidodipsas fischeri Boulenger

Tropidodipsas fischeri, Boulenger, *Cat. Snakes Brit. Mus.,* 2, (1894): 296 (substitute name for *Virginia fasciata* Fischer, 1885: 95 [type locality, Guatemala]); Mocquard, *in* Duméril, Bocourt, and Mocquard, 1908: 875, Pl. 54, Figs. 3 (1893), (Godines).

Tropidoclonium annulatum, Bocourt, *in* Duméril, Bocourt, and Mocquard, 1893: 738, Pl. 54, Fig. 3 (Godines).

Tropidodipsas annulata, Slevin, 1939: 407 (Chichavac).

Chichavac, C.N.H.M. Nos. 20257–60, 20272–74, 20519–20; Lorena, Nos. 100509(2), 100510(3), 100511; Tejutla, Nos. 98298–300.

This species is particularly characteristic of the oak-pine zone of the Guatemalan Plateau. It shows little habitat preference, as I have taken it in dry

TABLE X

Variations in Major Morphological Characters in *Tropidodipsas fischeri*

The number of keeled dorsals are listed for the neck and pre-anal region. The number for the cross bands on the body and tail are given as body/tail.

Number	Sex	Keeled Dorsals	Abdominals	Subcaudals	Labials	Bands	Lengths
98298	♂	15	177	53 + tip	6/7	42/13	500 + (90+)
98300	♂	5–7	168	48	6/8	49/15	520 (110)
100510A	♂	7	180	57	6/7–6	31/12	400 (80)
100510B	♂	9–11	183	62	6/7	42/16	510 (115)
C.N.H.M. 20257 ...	♂	7–11	170	55	6/7–7	37/10	500 (100)
C.N.H.M. 20259 ...	♂	?–9	182	57	7/7	40/?	495 (100)
C.N.H.M. 20272 ...	♂	9–11	181	49	6/7–6	43/12	285 (45)
C.N.H.M. 20274 ...	♂	3–9	182	64	6/7	41/15	490 (105)
C.N.H.M. 20519 ...	♂	11–13	173	59	6/7	47/19	395 (80)
98299	♀	11	170	49	6/7–6	40/11	655 (115)
100509A	♀	9–11	185	50	7–6/7	32/8	590 (95)
100509B	♀	7–9	187	50	7/7	48/13	580 (100)
100510C	♀	7–9	187	54	6/7	25/6	590 (100)
100511	♀	7	187	55	6–7/7	33/8	590 (100)
C.N.H.M. 20237 ...	♀	9–11	178	46	6/6	43/?	385 (60)
C.N.H.M. 20258 ...	♀	11–13	179	47	6/7	51/13	460 (70)
C.N.H.M. 20260 ...	♀	9–13	186	50	6/7–8	44/12	280 (45)
C.N.H.M. 20520 ...	♀	5–9	186	45	6/8–7	47/11	360 (55)

TABLE XI

Variations in Major Morphological Characters in *Bothrops godmani*

Number	Sex	Dorsals	Abdominals	Subcaudals	Labials	Lengths
100512	♂	21–19	135	26	10/11	645 (70)
C.N.H.M. 20264 .	♂	21–19–17	137	28	8–9/10–12	500 (60)
C.N.H.M. 20265 .	♂	21–19	134	28	10/12	600 (60)
C.N.H.M. 20269 .	♂	21–19–17	135	26	9/11	225 (25)
C.N.H.M. 20270 .	♂	21–19–17	132	27	9/11	....
C.N.H.M. 20646 .	♂	21–19–17	135	28 + tip	9/11	555 + (55+)
98321	♀	21–19–17	140	32	9/11	
C.N.H.M. 20266 .	♀	21–19	134	24	10/11	265 (25)
C.N.H.M. 20267 .	♀	21–19–18	136	25	9/11	390 (40)
C.N.H.M. 20268 .	♀	21–19–17	136	28	9–?/9–?	330 (35)
C.N.H.M. 20271 .	♀	21–19–17	132	22	10/11	375 (40)
C.N.H.M. 20645 .	♀	21–19–17	140	26	10/11	350 (45)

oak woods and from wet hillside marshes. Slevin (1939: 407) found the species beneath the bark of stumps in open areas, and I secured it in bromeliads at Lorena. It does not appear to range above about 2600 m. and descends to 1700 m. in the cloud forest facing the Pacific. It is apparently a nocturnal species which seeks deep shelter during the day.

All the specimens have 17 rows of dorsal scales throughout the body length, no praeocular, 2 postoculars (only 1 in No. 100510), temporals 1+2. A noteworthy variation which I am at a loss to explain, is the reduction in the number of cross bands in four of the six specimens from Lorena. Variations in major morphological features are presented in Table X.

Bothrops godmani (Günther)

Bothriechis godmanni, Günther, *Ann. Mag. Nat. Hist.,* 12 (1863): 364, Pl. 6, Fig. G (type locality, near Dueñas and the tableland of Guatemala, "Totonicapam" [Totonicapán] according to Boulenger, *Cat. Snakes Brit. Mus.,* III (1896): 546).

Bothriechis godmani, Günther, 1895: 190 (Totonicapán, Volcán de Fuego).

Lachesis godmani, Boulenger, 1896: 545 (Totonicapán, Volcán de Fuego).

Trimeresurus godmani, Mocquard, *in* Duméril, Bocourt, and Mocquard, 1909: 942 (San Lucas).

Bothrops godmani, Slevin, 1939: 412 (Chichavac).

Bothrops brammianus, Bocourt, *Ann. Sci. Nat.,* 10 (1868): 201 (type locality, San Lucas, 1558 meters).

Chichavac, C.N.H.M. Nos. 20264–71, 20645–6; Los Ocales, Skull uncatalogued; Tectitán (10 km. north of Tacaná), No. 98321; Yepocapa, No. 100512.

As is to be expected, this species, widely distributed throughout the highlands of Central America, is not uncommon on the southwestern highlands. In that area it appears to be restricted to the oak-pine zone. Slevin (1939: 412) secured it at 2600 m. in the Tecpán region, and I found it at slightly lower elevations in the Sierra Madre. The species is, however, unknown at Ixchiguán in the pine-cypress zone. This is rather surprising, since it has previously been reported from the Sierra de los Cuchumatanes at 3200 m. (Stuart, 1943*b*: 25–26). A summation of the major morphological features of the above series is given in Table XI.

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PLATE I

The high block of María Tucum looking southward toward the Pacific. The village in the right foreground is Totonicapán and Lake Atitlán appears in the left background. The horizon extends from the double volcano Fuego-Acatenango on the left (east) to the flanks of the Cerro Quemado on the right (west), a distance of 80 kilometers. The steep escarpment borders the rolling uplands of the surface of the mountain block. Through a gap between the volcanoes in the right background may be seen the edge of the Pacific coastal plain and the Pacific Ocean beyond. Drawn by William Brudon from a U.S. Army Air Forces photograph.

PLATE I

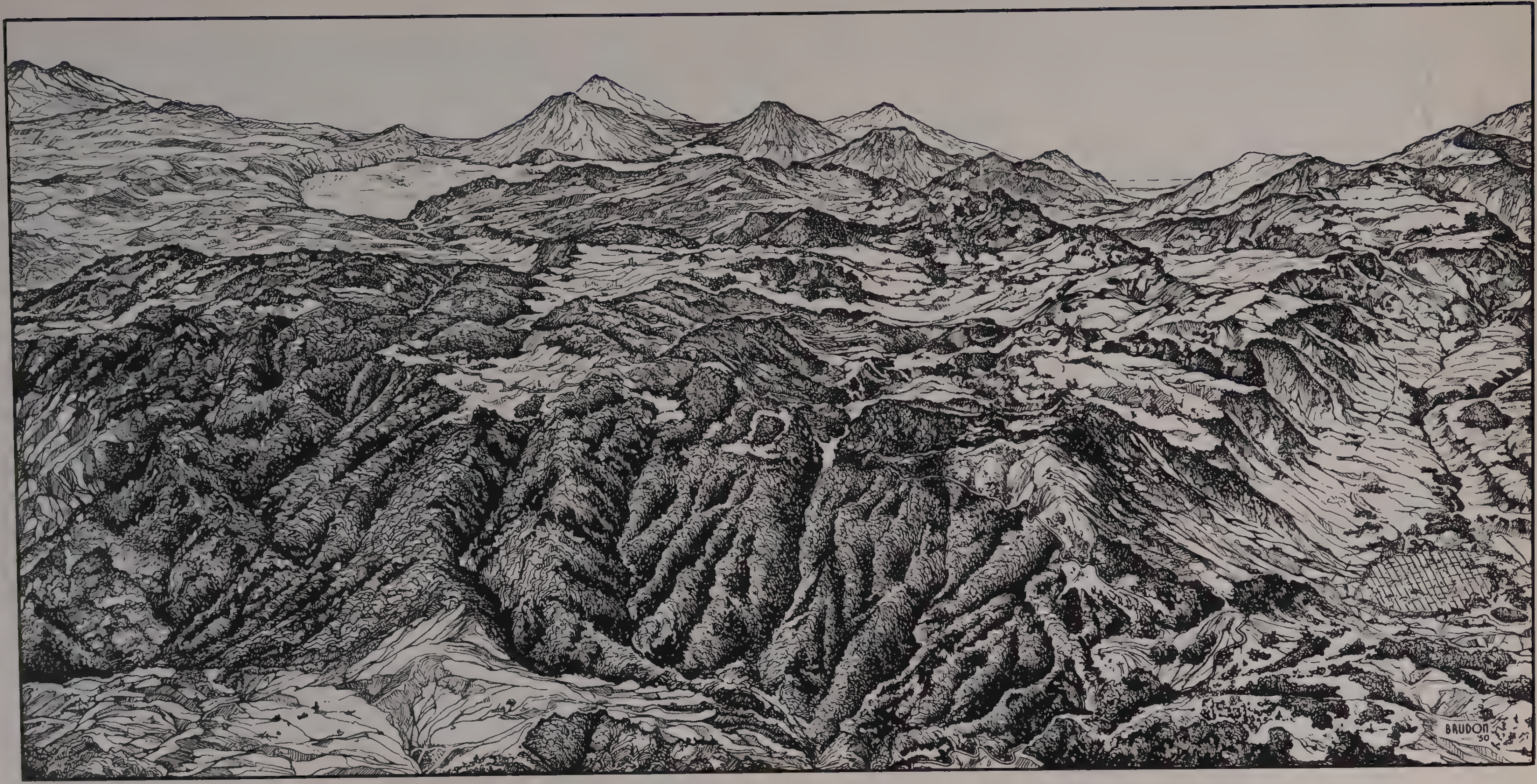


PLATE II

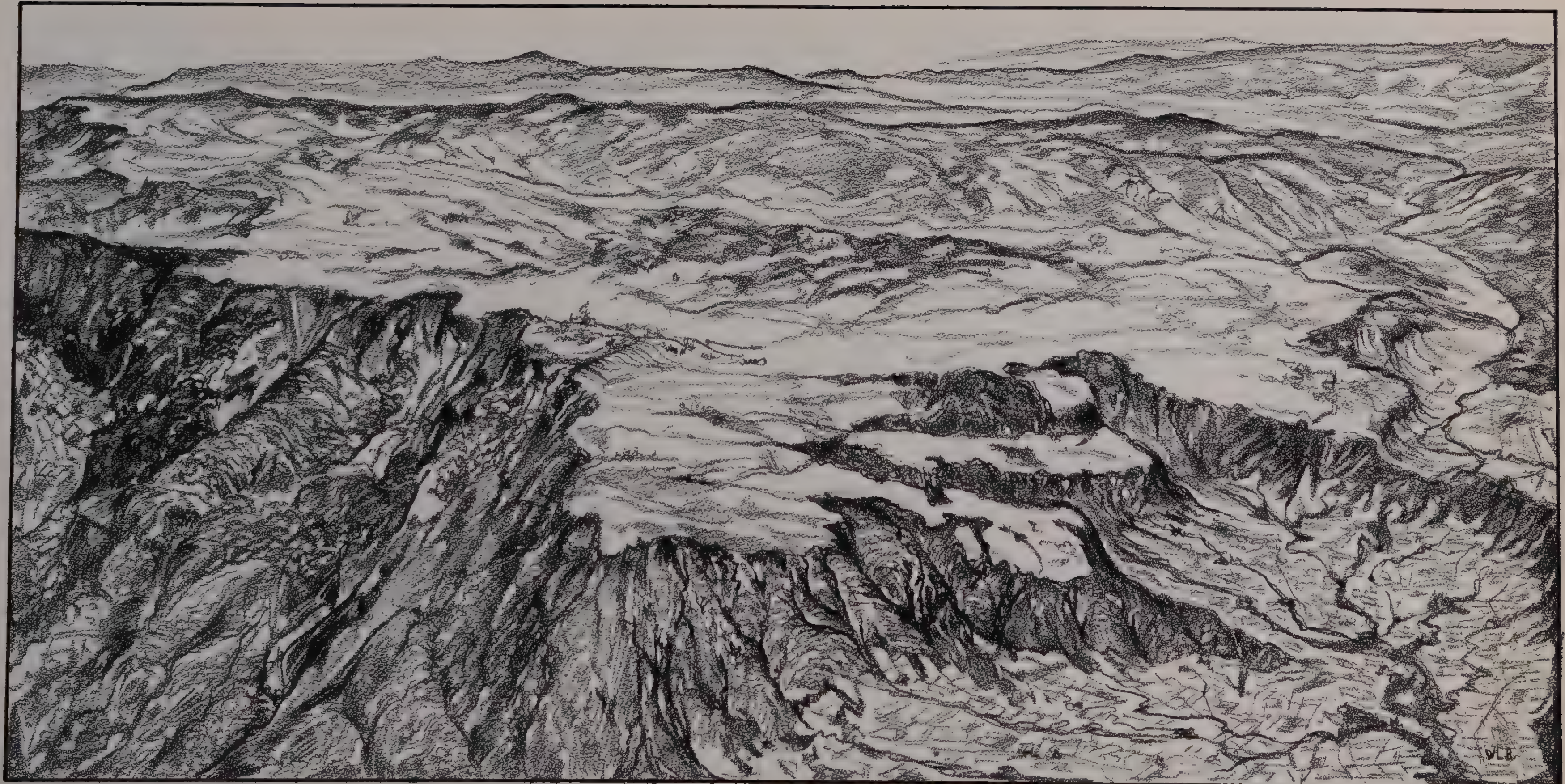


PLATE II

The Sierra Madre looking northward from directly above San Marcos. In the foreground are the steep escarpment slopes above which lies the rolling plateau surface. The depression in the middle distance on the plateau is the valley of the Río Cuilco headwaters that arise in the vicinity of Ixchiguán on the far left (west) of the plateau. Between the far margin of the plateau and the ranges on the horizon (Sierra de Cuilco on the left and the Sierra de los Cuchumatanes on the right) lies the deep valley of the Río Cuilco which, after cutting across the plateau from west to east, rounds the eastern end of the plateau. Cerro Cotzic is the peak on the far margin of the plateau to the left. Tacaná is hidden behind the western margin of the plateau. Tejutla lies near the eastern end of the Río Cuilco headwaters as they emerge from the plateau. The east-west distance on the horizon is about 90 kilometers. Drawn by William Brudon from a U.S. Army Air Forces photograph.

PLATE III

Fig. 1. Northwestward across the bunchgrass *(pajón)* plains of the Sierra Madre from Serchil. The highest point on the ridge in the background is Cerro Cotzic. June 21, 1947.

Fig. 2. Bunchgrass on the flanks of Cerro Cotzic just north of Ixchiguán. The regular plots of short grass are areas from which the bunchgrass has been removed for potato cultivation. Short grasses are the first plants to invade such plots following their abandonment. From the base of the bunchgrass plants were taken specimens of *Pseudoeurycea rex, Magnadigita rostrata,* and *Barisia m. rafaeli.* The source of the stream in the foreground, the Río Cuilco, is the type locality of *Plectrohyla cotzicensis.* It lies several kilometers upstream (to the left) from this point. Specimens of *Sceloporus m. smaragdinus* occurred in tremendous numbers among the rocks along the stream. August 25, 1947.

PLATE III

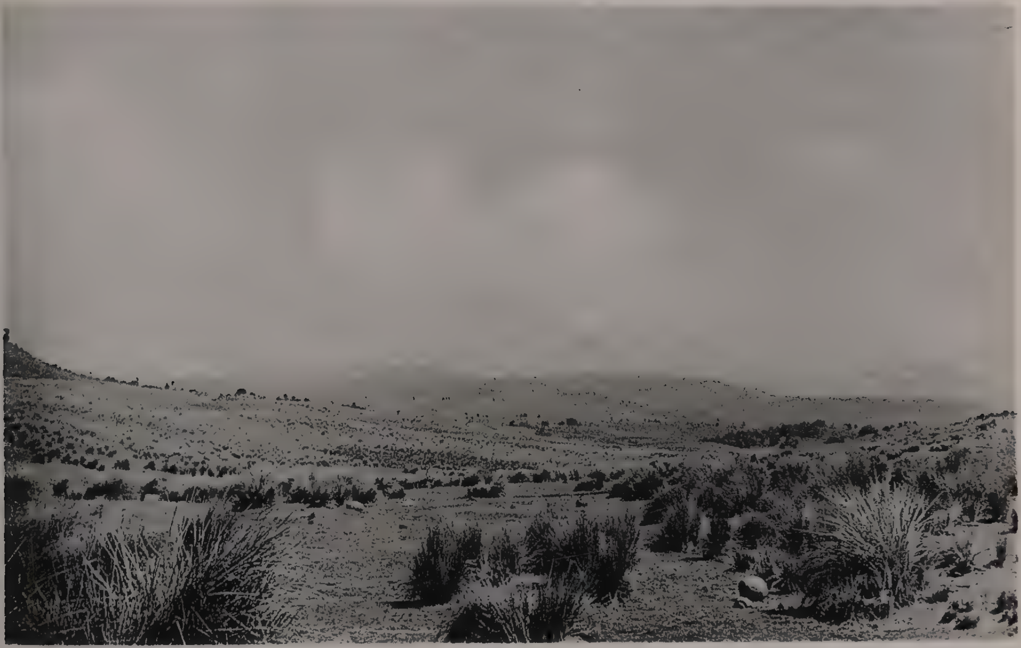


FIG. 1

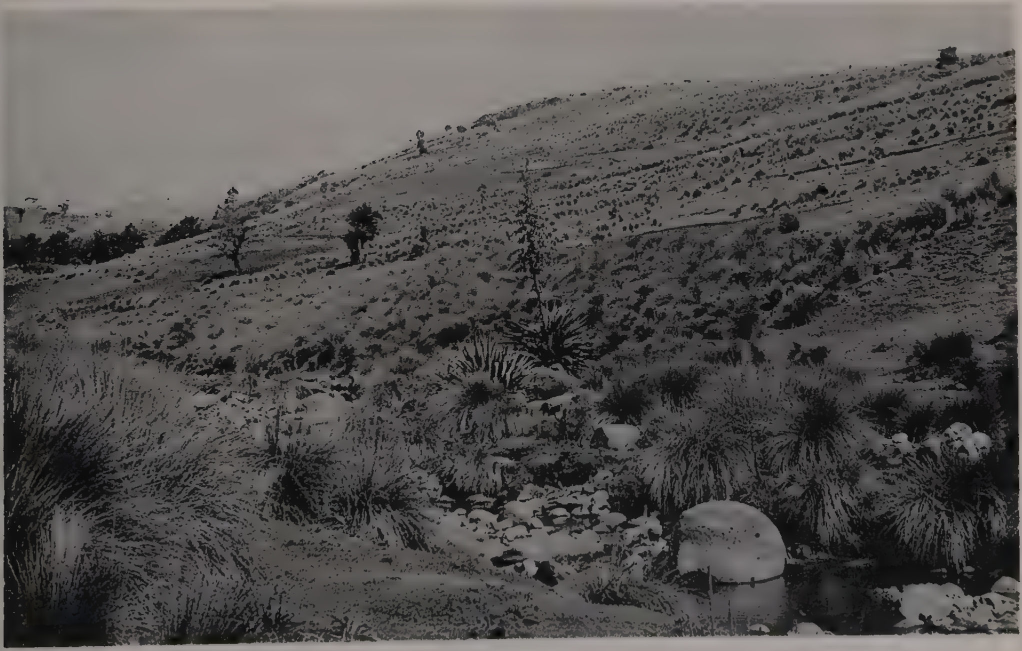


FIG. 2

PLATE IV

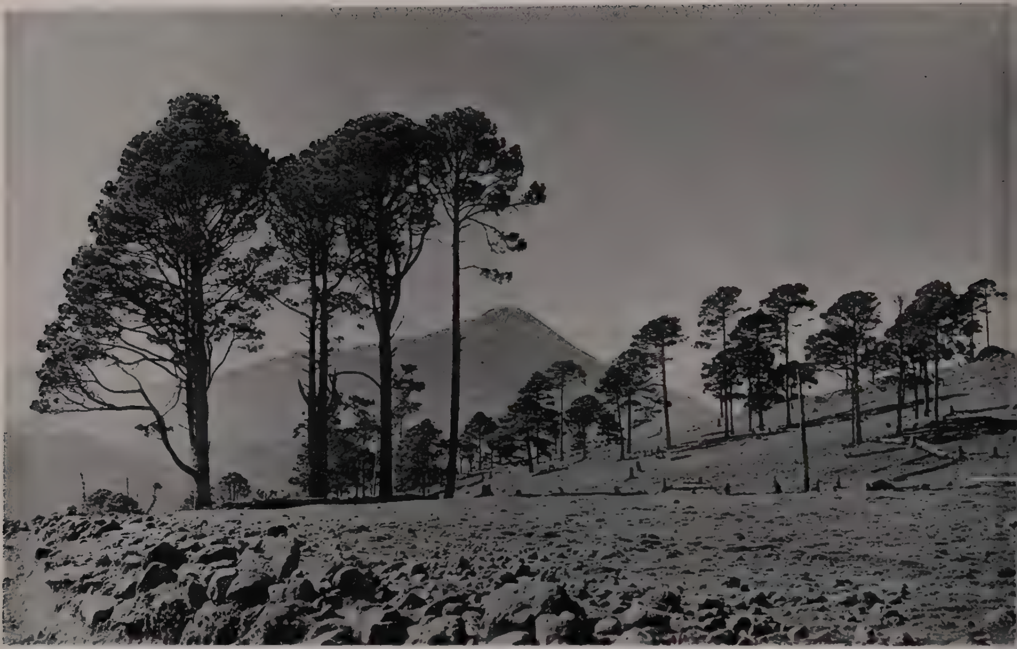


Fig. 1

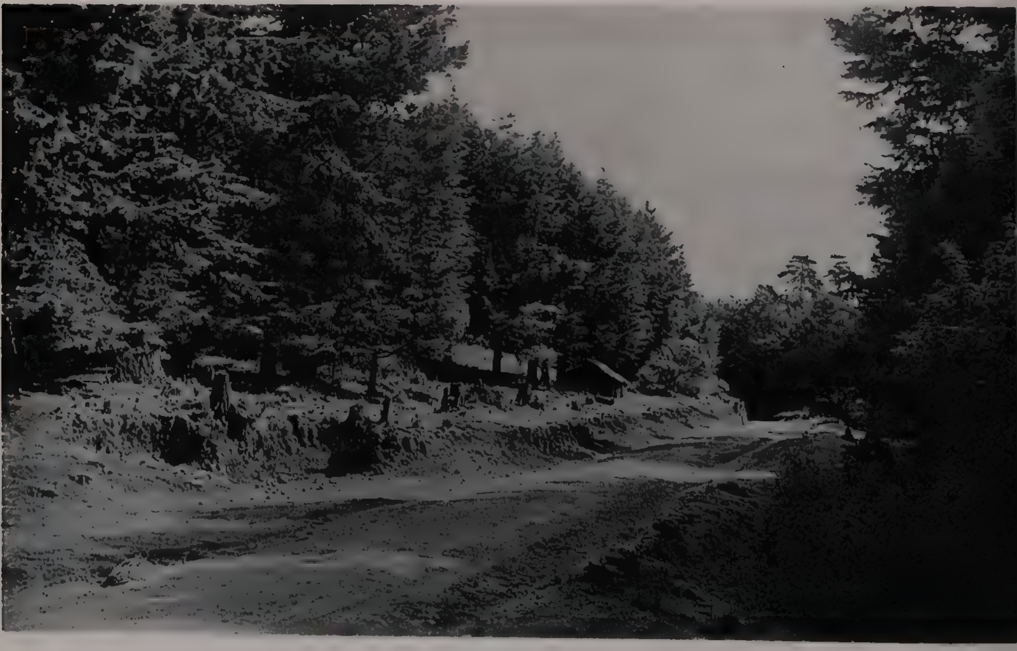


Fig. 2

PLATE IV

FIG. 1. Short grasses and scattered pine on Cumbre Cotzic (3600 m.). Among the rocks in the foreground *Sceloporus m. smaragdinus* was abundant; under the logs in the background *Pseudoeurycea rex* was common. In the extreme background is Volcán Tajumulco viewed from the north. April 8, 1947.

FIG. 2. A road through the pine-cypress forest at Serchil. Specimens of *Sceloporus m. smaragdinus* were abundant along this road. June 21, 1947.

PLATE V

Fig. 1. Within the pine-cypress forest at Serchil. Only *Pseudoeurycea rex* was found in this habitat. June 21, 1947.

Fig. 2. Rolling uplands in the vicinity of Tejutla. This condition of forests broken by cultivated openings is typical of most of the oak-pine zone of the southwestern highlands. Although almost entirely of pine, oak is common in the understory. Early April, 1947.

PLATE V

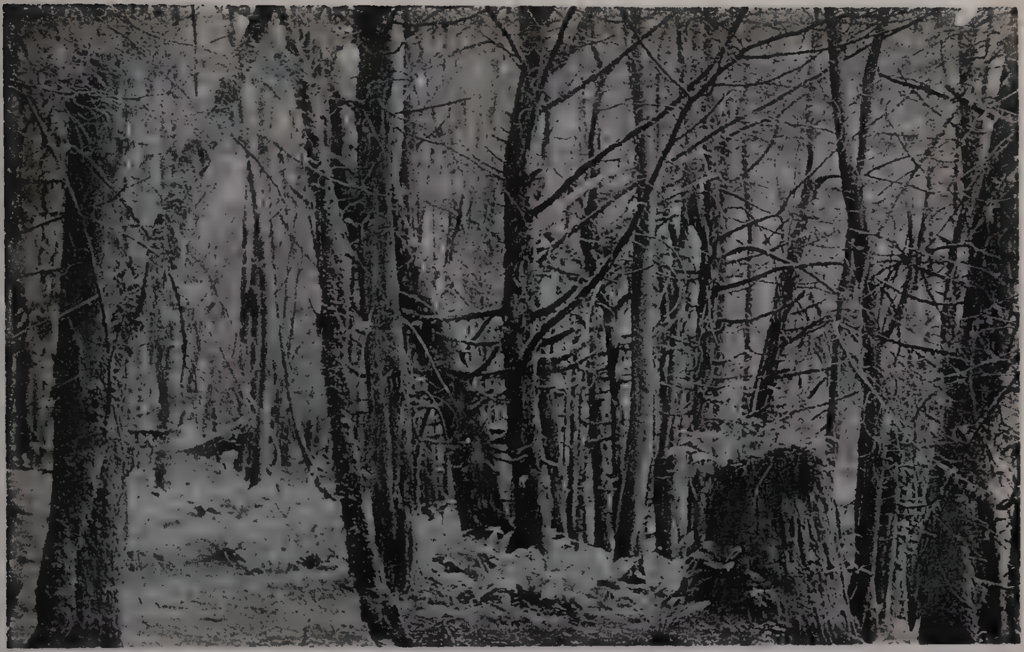


Fig. 1

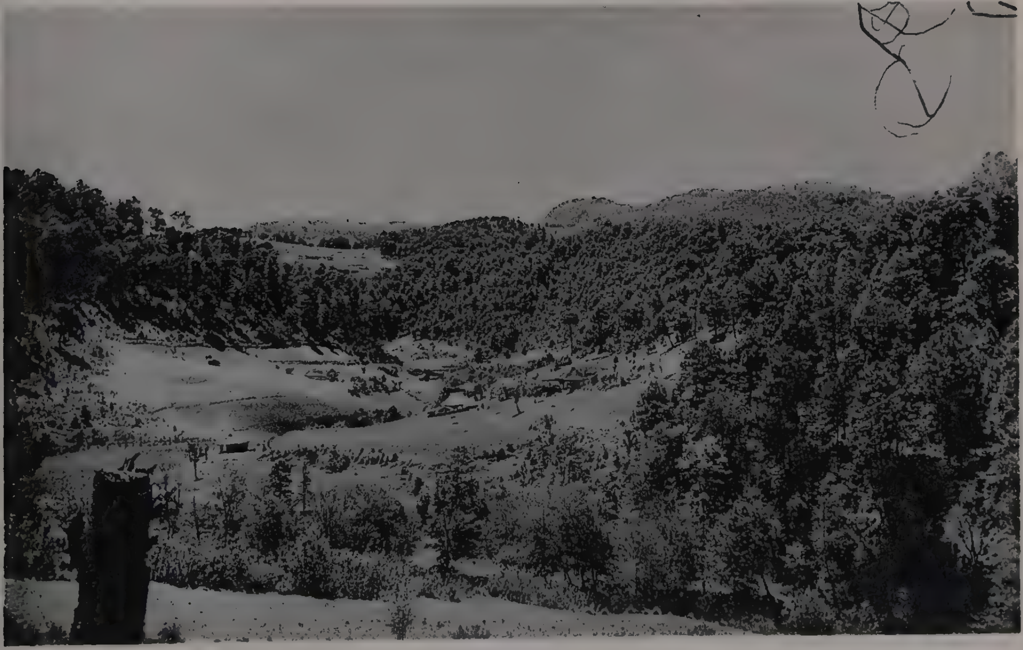


Fig. 2

PLATE VI

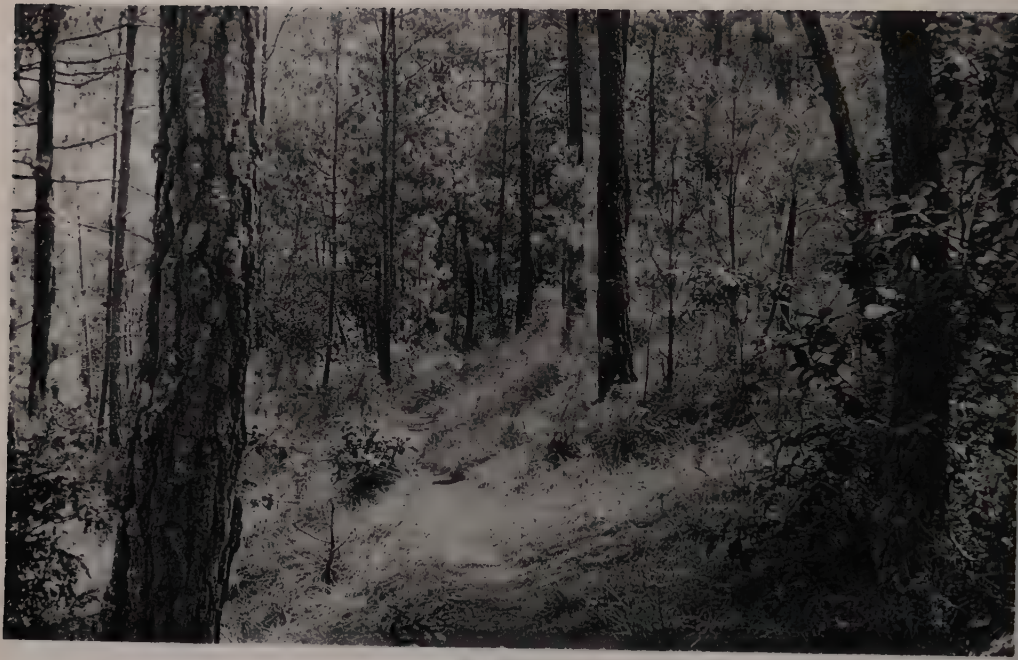


Fig. 1

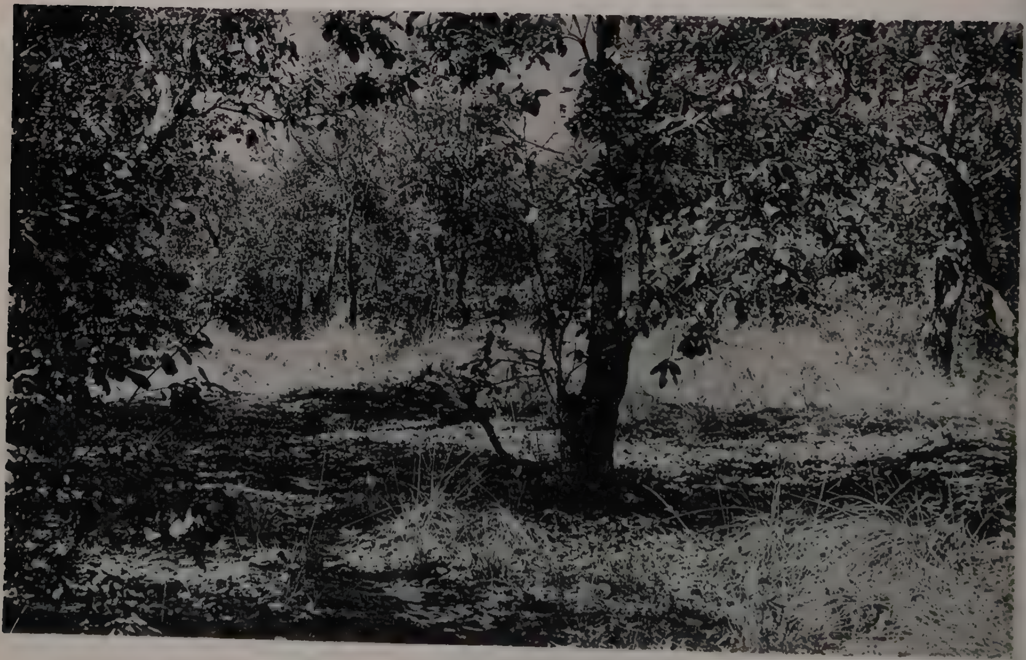


Fig. 2

PLATE VI

FIG. 1. Pine forest in the vicinity of Momostenango. Note the scanty undergrowth. In many such forests a ground cover is completely lacking and the forest floor is deep in pine needles. Only rarely are reptiles encountered. June 27, 1947.

FIG. 2. Oak grove in the valley of the Río Cuilco at Tejutla. Note the relatively heavy layer of fallen leaves in the shade of the trees. In such groves both *Sceloporus m. smaragdinus* and *Anolis c. crassulus* occurred sparingly; within the leaf layer *Bufo bocourti* and *Tropidodipsas fischeri* were occasionally encountered. Such stands of pure oak are relatively uncommon on the southwestern highlands. April 2, 1947.

PLATE VII

Fig. 1. Tadpole of *Rana macroglossa*. Lateral view.

Fig. 2. Mouthparts of a not quite fully developed tadpole of *Rana macroglossa*.

Fig. 3. Mouthparts of the fully developed tadpole of *Plectrohyla cotzicensis*.

PLATE VII

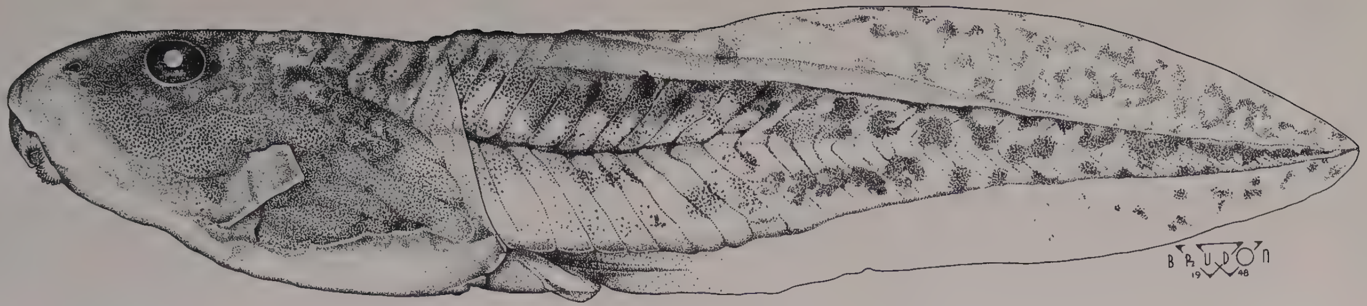


Fig. 1

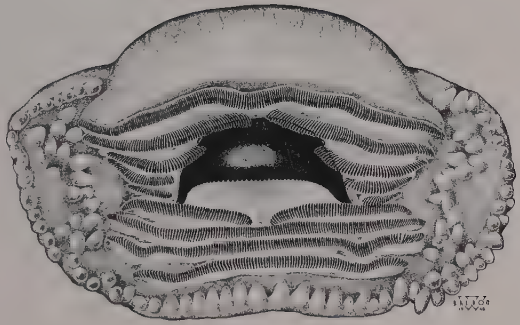


Fig. 2

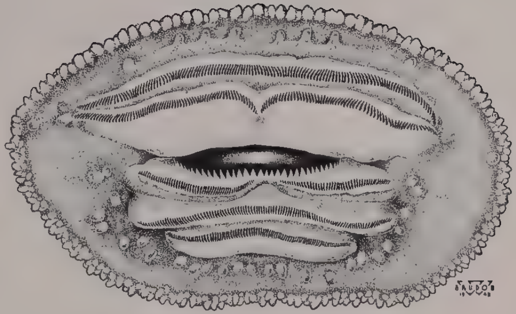
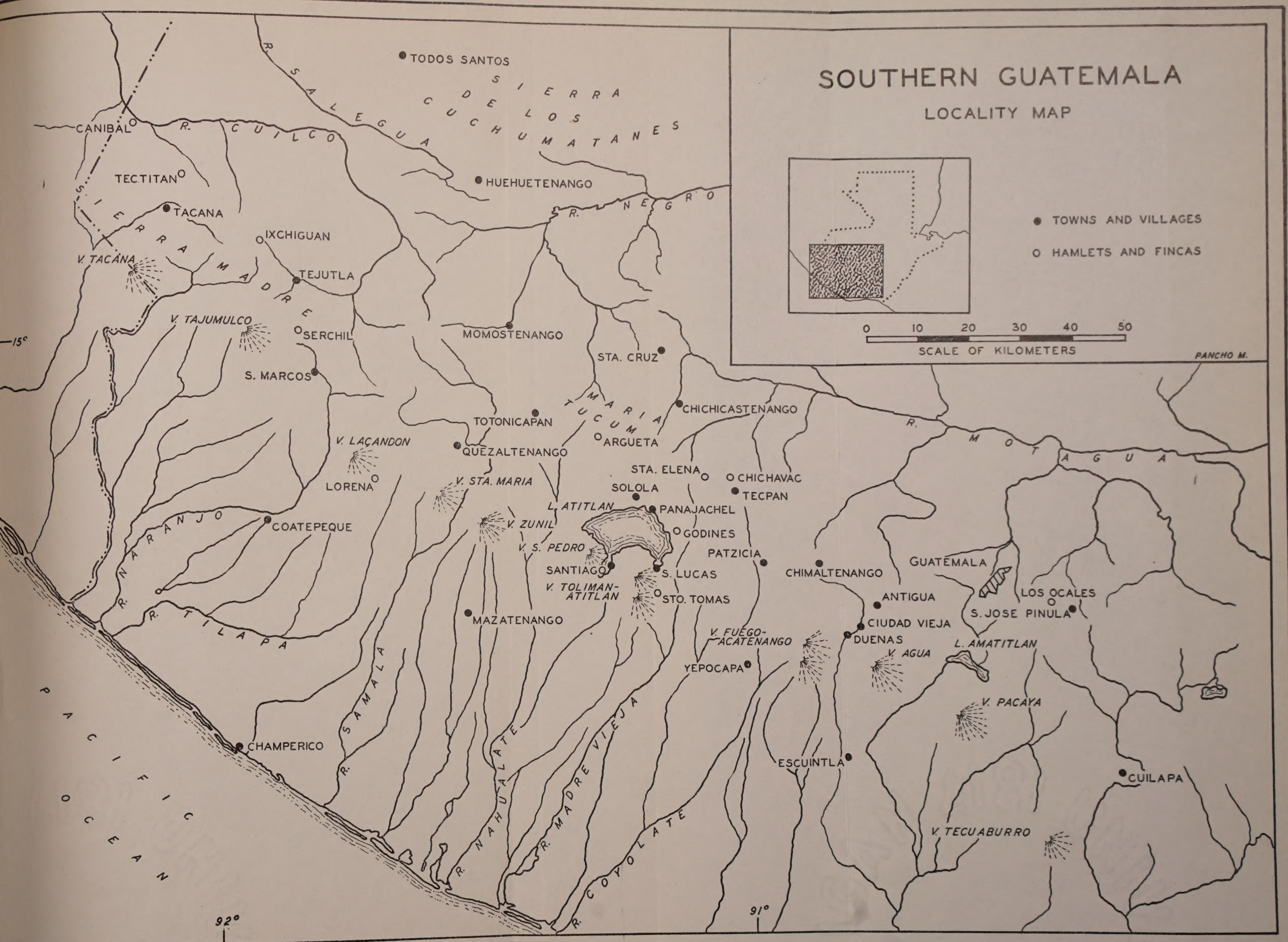


Fig. 3



Map. 2. Southern Guatemala, with particular reference to collecting stations on the southwestern highlands.